A STUDY OF
THE POPULATION DYNAMICS
OF THE MALLEE
EUCALYPTUS INCRASSATA LABILL.

by

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of Doctor of Philosophy in the
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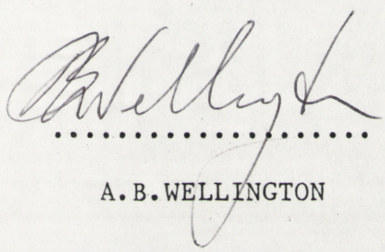
STATEMENT

The work presented in this thesis is my own. Specific contributions by others have been referred to in the text and acknowledgements.



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" During all our extensive wanderings in Raak, as in the neighbourhood of Lake Mournpool, not a single young plant, if we omit the Weeping Pittosporum, of any of the trees or shrubs met with was noticed. Fire seldom or never ravages the district, and the depredations of stock are unimportant or negligible. One is prompted to ask. Why is this so? "

(O'Donoghue (1916) "Rambles in Raak"
Vict. Nat. Vol. XXXIII, p23.)

ABSTRACT

A multi-stemmed form of Eucalyptus known as "mallee" occurs in semi-arid, southern Australia. The capacity for vegetative regeneration from buried lignotubers, especially after fire, and a paucity of seedlings, has led to speculation that mallees are long-lived and that recruitment is presently insignificant. However, radiocarbon dating shows that mallees, like other eucalypts, are not long-lived (life-span: <400 years).

A study of the population dynamics of the mallee Eucalyptus incrassata was carried out at a site of recent recruitment following a fire (in December 1977) in the Big Desert in semi-arid, north-western Victoria. Individuals ('genets') in the population were classified into 'life stages': rates of movement of genets between successive life stages, rates of genet mortality, and the processes controlling these rates, were investigated.

Canopy seed stores were spatially and temporally variable. Seed release from the canopy occurred intermittently throughout the year (ca 70 seeds $m^{-2}year^{-1}$ under fecund canopies). Fallen seeds were rapidly removed by ants. Although buried seed can remain viable for at least one year in unburnt stands, there was no natural soil storage of seed in the stands investigated.

E. incrassata seeds were dormant under high temperature conditions (30°C) but germinated readily at lower temperatures (>90% germination on filter paper, ca 50% germination in soil). Some natural germination occurred in unburnt stands during winter 1980 ($<10^2$ ha^{-1}) but none of the germinants survived to December 1980.

Experimental release of canopy seed stores, as occurs after fire, resulted in soil storage of seed in an unburnt stand. This phenomenon may have resulted from predator satiation due to the sudden, massive increase in seed presence on the soil (ca 300 seeds m^{-2}).

Factors associated with fire-induced changes to the soil (i.e. heating and ash addition) caused an increase in both germination rates, and total percentage germination. Minimum recruitment rates following the December 1977 fire were estimated at 10^4 seedlings ha^{-1}.

Mortality of new genets was greatest at higher positions on dunes and least in swales for areas of similar genet density. Density-dependent mortality was consistently high on the upper slopes of dunes, but varied between successive years for lower dune slopes and

swales. Mortality of new genets was confined to summer when prolonged, dry periods occurred. Experimentally-applied increases of soil moisture and nutrients significantly reduced mortality rates in areas of high juvenile density. Measurements made in February and March 1980 after three months of drought showed that many juveniles were drought-stressed whereas surrounding adults (coppicing lignotubers) were not. Low soil moisture levels were an important cause of early genet mortality.

Post-fire genet densities (10^4) were higher than pre-fire genet densities (ca $3x10^2$ ha^{-1}). Adult mortality rates were low in long-unburnt stands (0.6% in two years) but were higher at recently-burnt sites (5.0% in two years). Mortality rates of new genets in the two years following the fire were high (ca 75%). These estimates conform to a Deevey Type III survivorship curve.

Fire plays an important role in the population dynamics of the mallee E. incrassata by inducing soil storage of seed as a result of predator satiation, by enhancing germination, and by increasing adult mortality. The rare coincidence of both fire and years favourable for seedling establishment results in episodic recruitment events which are widely spaced in time, giving a steady-state appearance to mallee populations.

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CHAPTER ONE

INTRODUCTION

CHAPTER 1

INTRODUCTION

1.1 The dynamics of plant populations

Demographic studies are concerned with the statistics of births, deaths, diseases etc. which illustrate the life conditions of communities (The Oxford English Dictionary, 1933). Until recently, few demographic studies had been carried out on plant populations. Harper (1967) attributed this shortfall primarily to difficulties associated with two interrelated properties of higher plants, viz: plasticity of growth, and vegetative reproduction. As a result of these properties, it is often difficult to determine exactly what constitutes a genetic individual (or 'genet') for many species of plants (Harper 1977).

The majority of recent plant demographic studies have been made on annuals and short-lived perennials; generally the species selected are those in which the nature of a genet is clearly definable. Studies on clonal plants and long-lived perennials have been few and incomplete, often concentrating only on the dynamics of selected plant organs (or 'ramets'), or on a particular stage of the life-cycle. As a consequence, the generalizations drawn from demographic studies of plants have been biased towards short-lived species. Further studies of clonal plants and long-lived perennials are necessary to provide a more comprehensive basis for our understanding of plant population dynamics.

1.2 The mallee habit

In Australia, many species of the genus Eucalyptus occur in fire-prone environments. With very few exceptions, these species have evolved a specialized, semi-subterranean regeneration organ called a "lignotuber" (Kerr 1925). The lignotuber contains reserves of dormant buds and stored food materials (Chattaway 1958a). By virtue of its position, and a relatively thick bark on its exposed surfaces, the lignotuber is capable of surviving severe fires (McArthur 1968). It therefore provides the plant with an effective means of vegetative regeneration (Chattaway 1958b).

In most eucalypt species, the lignotuber is only important in the early stages of the life-cycle. It is eventually incorporated into the growing stem, which then assumes a compensatory regeneration capacity through the development of numerous, dormant, epicormic buds. The epicormic buds in the trunk and lower branches are protected from fire damage by an insulating layer of bark (Gill 1975).

In some eucalypt species that occur in particularly harsh environments, the lignotuber continues to develop and is retained as an important part of the mature plant. These species are called "mallees", an aboriginal term referring to their unique growth habit (Kenyon 1914). Mallees are generally stunted, multi-stemmed shrubs ranging from 2m to 12m in height. The lignotuber may be quite large: Mullette (1978) has described a mallee form of Eucalyptus gummifera with a lignotuber covering an area of $75m^2$. However, in more arid areas, where mallee species form the dominant vegetation, the lignotuber rarely exceeds 2m diameter, and is usually much smaller (<1m).

1.3 The mallee habitat

1.3.1 Introduction

Mallee forms of Eucalyptus occur in a wide range of habitats. Of the ca 400 species of Eucalyptus described by Pryor and Johnson (1971), approximately 130 species are known to adopt a mallee habit (Specht 1972). The mallee growth form is usually associated with adverse environments (Gill 1975), and many species which occur as mallees are found as forest trees in more favourable habitats, e.g. E. gummifera (Mullette 1978). Some species are known to adopt a mallee habit exclusively. However, these are relatively few in number, and are confined in their distribution to southern, semi-arid regions of the continent (Burbidge 1952). Areas dominated by mallees are generally referred to as "Mallee areas", or "the Mallee".

Although much of the original vegetation of the Mallee has been cleared for agriculture, some comparatively undisturbed stands are still to be found in nature reserves, national parks and areas generally unsuited for cultivation. These undisturbed stands are most common on the arid fringes of Mallee areas and in regions characterized by soils of extreme nutrient deficiency.

1.3.2 Origins and present distribution

Mallee areas once extended from Western Australia across the southern fringes of the Nullabor Plain into South Australia, and finally into south-western New South Wales and north-western Victoria (Parsons 1970). The general paucity of mallee eucalypts in the arid centre, particularly in refugial areas, as well as their absence from northern Australia, has led to speculation as to a relatively recent origin of

this morphological form within the genus Eucalyptus (Burbidge 1952). An examination of the distributions of a variety of species occurring in mallee vegetation provides some evidence that the centre of development of this vegetation type was in southern Western Australia (Burbidge 1952). Subsequent migrations eastward associated either with climatic changes, or with sea-level changes, may have led to its present distribution (Parsons 1970).

Mallee vegetation presently occurs in areas lying between the 200mm and 500mm isohyets (Wood 1929, Jessup 1946), and tends to predominate only in those regions with greater than 250mm mean annual rainfall (Parsons 1970). Water appears to be a major factor in determining the boundaries of mallee, which has been described as forming a broad transition zone between the eucalypt forests of wetter areas and the Acacia-dominated shrublands and the grasslands of the arid centre (Specht 1972). Mallee communities therefore occur at the most arid extremes of the range of distribution of the genus Eucalyptus.

1.3.3 Climate

The climatic regime of Mallee areas is characterised by warm to hot summers and cold winters. Temperature extremes may exceed 40°C for periods of several days in summer. Winter temperatures are low enough to limit plant growth, and frosts are common (Holland 1969c).

Rainfall tends to be distributed evenly throughout the year, with a slight winter maximum in southern areas but a trend towards summer maxima at the northern limits of distribution. Summer rainfall is often very erratic and drought periods of one or two months duration are not uncommon (Leeper 1970).

The climate of Mallee areas has been broadly classified as a mediterranean type, although the probability of summer drought is sufficiently high that the climate is often described as a modified mediterranean type (Leeper 1970).

1.3.4 Pedology and geomorphology

The soils of the Mallee region are generally of aeolian origin. They are often calcareous or saline, and are of low nutrient content (Specht 1972). Characteristic soil types have been classified as 'solonized brown' soils and 'solodized solonetz' soils (Stace et al. 1968). However, the vegetation type embraces an enormous variety of soil types, ranging from shallow, calcareous, very heavy clay soils to deep siliceous sands with little profile development (Specht 1972).

Geomorphologically, much of the area dominated by mallee comprises aeolian sand ridges interspersed with swales of varying sizes. Dune systems are predominantly regular. Occasional large plains, formed as a result of fluvial and lacustrine processes, also occur (Hills 1939, Lawrence 1966, Bowler and Magee 1978).

1.4 Mallee vegetation

Mallee vegetation forms a broken canopy which has been described as a mosaic of shrub thickets and large openings (Holland 1969b). Specht (1972) classified this vegetation type as an "open scrub formation". The structural divisions of thickets and openings are static at all times of the year, imposing a rigid pattern on the vegetation (Holland 1967). The areas beneath thickets have been shown to possess a rich

flora relative to areas between thickets; the latter are often bare for all but the spring months (Holland 1969b). Litter tends to accumulate beneath the thickets, and eventually forms a soil nutrient halo around each thicket (Burrows 1976). The increased nutrient levels beneath thickets may account for the richer thicket flora reported by Holland (1969b).

The areas between thickets are often extensively colonized by lichens and mosses, forming a soil crust. Experiments conducted by Ioannou (1968) indicated that intact soil crusts may inhibit germination both by increasing rates of absorption of surface water into the soil, and by forming a hard surface which the radicles of newly-germinated seeds have difficulty in penetrating.

Components of the understorey are variable, ranging from sclerophyllous shrubs of varying densities in the wetter localities, to grass hummocks of Triodia on the deep sandy plains and ridges of the drier areas. In the more arid, northern regions, semi-succulent shrubs, mostly chenopods, occur. Intergradings of these different understory forms are common; their relative presence within the limits of the mallee system appears to be related to water and edaphic factors (Specht 1972).

There have been several floristic classifications made of mallee vegetation (see for example: Zimmer 1946, Beadle 1948, Stannard 1958, Noy-Meir 1970, Specht 1972). Holland (1967), in reviewing some of this work, concluded that the phytosociological status of mallee communities was not well understood. The work of Noy-Meir (1970, 1971, 1974), with its very broad survey base and its consideration of edaphic variation, probably represents the most comprehensive classification to date. Other detailed studies investigating the relationship between mallee

communities and their edaphic environments (see El-Ghonemy 1966, Parsons 1966, Burrows 1976) highlight the importance of soil factors in determining the composition of the community.

1.5 Mallee recruitment

Seedlings of mallee eucalypts are absent from most mallee populations. For many years, there was some controversy as to whether seedlings of mallee eucalypts ever occur under present climatic conditions. An article by Pescott (1941) posed the question: "Is the seed of Mallee Eucalypts germinable?", and went on to note that "for many years claims have been made, in many quarters, that the seed does not germinate." He noted further: "these claimants asserted that whenever alleged seedlings have been found it was always possible to trace the small roots right down to an old underground root." In an effort to clarify the situation, Pescott (1941) placed an advertisement in a farmers' newspaper from the Mallee region of Victoria inviting correspondence from anyone who knew of naturally-occurring seedings. This advertisement elicited a number of replies noting instances of natural recruitment of mallees. Three of the replies are discussed by Pescott (1941), and it would appear from a consideration of these that mallee seedlings do occur under natural conditions. Pescott (1941) concluded his article by presenting evidence of the germinability of seeds from eight species of mallee.

However, previous reports (Zimmer 1940a, 1940b) had already noted the ready germinability of mallee seeds, the ease with which seedlings can be raised under nursery conditions (Zimmer 1940a), and the existence of naturally-occurring seedlings in a recently-burnt area (Zimmer

1940b). Pescott's (1941) article elicited a further report (Zimmer 1941) presenting other examples of these phenomena.

Since 1941, there have been more published reports of the occurrence of seedling regeneration in mallee. Sims (1951) described three instances of germination and establishment of mallee eucalypts. In each of these instances, mallee stems had been cut and placed across sand drift areas in an attempt to stabilize the substrate. Germination of mallee eucalypt seedlings occurred in the areas immediately beneath these stems. In one instance, the seedlings were still alive six years later and had developed into "flourishing bushes up to five feet tall" (Sims 1951).

Holland (1967) apparently misinterpreted the published evidence (Zimmer 1940a, 1940b, 1941, Pescott 1941, Sims 1951), since he observed that "... there is no record in the literature of naturally occurring mallee eucalypt seedlings." However, in a later article (Holland 1969a), he recorded seedlings which were establishing in a recently burnt area close to one of his study sites. A further report of the occurrence of seedlings in a recently burnt area near Hattah in Victoria was made by George (1974). Mallee seedlings have also been reported as establishing in areas of soil disturbance (Ioannou 1968), and from seed artificially sown in a long-unburnt mallee stand (Parsons 1968).

While reports in the literature establish beyond doubt that natural seedling regeneration of mallees does occur under present conditions, it is also apparent that recruitment is not common. The paucity of natural seedling regeneration, together with the well-developed capacity of the lignotuber for vegetative regeneration, has led to speculation on the longevity of mallees (Holland 1968, Gill 1971, Ogden 1978) and raised questions as to the nature of, and the factors controlling, the dynamics

of mallee populations (Parsons 1968a, Holland 1968,1969a).

1.6 Population biology of mallee eucalypts

The majority of previous studies of mallee vegetation have been largely descriptive (see Section 1.4). However, there have been two detailed investigations of processes operating in the mallee ecosystem. These investigations have been concerned with dynamics of above-ground ramets and litter production (Holland 1967), and with nutrient cycling (Burrows 1976). Such studies provide insight into the way mallee eucalypts respond to their environment in terms of growth and nutrient-turnover, but shed little light on the nature of mallee dynamics or the processes controlling them.

The intriguing questions raised in Section 1.5 concerning mallee recruitment and longevity prompt a demographic study of mallee populations. It seems important to ascertain a better understanding of mallee dynamics for other reasons as well. Mallee vegetation presently covers large tracts of land in the semi-arid regions of southern Australia. Much of this relatively undisturbed area is incorporated in national parks and other areas controlled by organizations concerned with environmental management. The mallee communities of these areas form the preferred habitats of many interesting and unique species (e.g. the Mallee Fowl - Leipoa ocellata). It is crucial to their continued survival that the mallee habitat be maintained in a viable, natural state. Such a charter necessitates sound management policies; the fundamental basis for such policies must lie in a thorough understanding of the dynamics of the vegetation.

There are also economic reasons for a study of the population biology of mallees. Large tracts of mallee near the lower rainfall limits of its distribution are classified as 'marginal' (Meinig 1962) since the rainfall is either too low or too erratic for the land to be used for agronomic purposes. For many years, much of this marginal land has been used for grazing, although the carrying capacity is low (<1 sheep per 10ha). In an attempt to improve the carrying capacity of mallee areas, a C.S.I.R.O. program of long-term experimental work is underway. Investigations are being made of the effects of different fire regimes with a view towards increasing the herbaceous component of the ground flora by opening up the canopy (Noble et al. 1980). A study of mallee population dynamics might enable a more rapid development of suitable management strategies with their concomitant economic benefits.

For the reasons outlined above, a study of the population dynamics of mallee eucalypts was undertaken. The aims of the study were:

1. to investigate genet (lignotuber) ages;
2. to monitor mortality of genets over a short (2 year) time period;
3. to ascertain the factors controlling recruitment and mortality of mallee populations.

CHAPTER TWO

APPROACHES TO A STUDY OF MALLEE DYNAMICS

CHAPTER 2

APPROACHES TO A STUDY OF MALLEE DYNAMICS

2.1 Introduction

Conventional approaches to the study of populations commonly involve a life table analysis (Deevey 1947). The life table summarizes population age structure, and therefore describes the manner in which life-expectancy changes with age. Most life table analyses require that populations have stable age structures. However, many populations do not have stable age-specific birth and death rates, and therefore their age structures are unstable in time. For these populations, alternative approaches must be used in an investigation of their population dynamics.

Disturbances such as fire, flood and drought can have a profound effect on the dynamics of plant populations, influencing recruitment, mortality, dominance and size distributions (Harper 1977). Disturbance regimes are often stochastic, and thus many populations occurring in disturbance-prone environments have unstable age structures. Mallee eucalypts occur in environments subject to the stochastic effects of fire and drought (Chapter 1). Mallee recruitment appears to be episodic, and confined to recently-burnt sites. It therefore appears likely that mallee populations do not have stable age structures, and that a life table analysis is not a suitable technique for a demographic analysis of mallees.

For plant populations with unstable age structures, a knowledge of genet ages can provide important information on aspects of population behaviour (e.g. whether episodic recruitment leads to even-aged stands, whether gap replacement occurs from an advanced seedling pool, whether recruitment is continuous, whether a positively- or negatively-skewed survivorship curve is characteristic for a particular species, etc.). The determination of genet ages may be particularly useful in the case of long-lived perennials, where it is not feasible to monitor survivorship of cohorts throughout their life-cycle.

The mallee habitat is subject to recurrent fire. A fire in a mallee population generally kills the above-ground stems, and new stems eventually develop from dormant buds in the lignotuber. This phenomenon results in many populations having stems of younger age than the lignotuber. Analyses of lignotuber ages would therefore be necessary to determine genet ages. Several techniques for ageing mallee lignotubers were investigated in the present study; the results of these investigations are described in the following sections.

2.2 Growth ring analysis

2.2.1 Introduction

Analyses of growth ring phenomena may be used to age woody perennials (Fritts 1976). Growth rings are formed in most species of woody plants. In many species the ring structures result from periodic fluctuations in growth, which may be endogenous or related to environmental factors. Sequences of ring widths often reflect temporal variations in climate, and in particular are influenced by rainfall and temperature (Fritts 1976). Other factors which affect the vitality of a plant (e.g. insect grazing, Morrow and La Marche 1978) may also be

important in determining ring width.

Tree-ring analyses have been carried out on mallee stems (see Holland 1967, Burrows 1976). For some sites, a good correlation was found between stem age as estimated from ring counts, and time since the last recorded fire at the site. However, Holland (1967) noted variable growth in different stems of a single plant. Peripherally-located stems from some lignotubers did not accrue detectable growth rings during the three years of Holland's (1967) study, while centrally-located stems on the same lignotubers, added annual rings. Similar observations of variable stem growth in multi-stemmed plants have been made by Fritts (1976).

There have been no published studies investigating ring structures in mallee lignotuber wood. An attempt was made in the present study to estimate lignotuber ages using ring analysis techniques.

2.2.2 Methods

Ten lignotubers of varying size were sectioned in both transverse and longitudinal planes. These sections together with transverse sections from the stems on each lignotuber were polished and examined with a stereo-microscope.

2.2.3 Results and discussion

Some ring patterns were evident in both lignotuber and stem sections when examined with the naked eye. Microscopic examination of the sections revealed that whereas the stem wood was 'ring-porous' and showed a reduction in xylem vessel size from earlywood to latewood, the lignotuber sections were 'ring-diffuse' and exhibited similar-sized

vessels throughout (see Fritts 1976, pp 60-63). As a result, ring structures in the lignotuber wood, which appeared visible to the naked eye, were no longer evident under magnification.

Ring counts were attempted along at least five radii for each of the sections of lignotuber wood. Large variations in ring counts (up to 80%) were found between radii from the same section. This phenomenon was accentuated by the lobular growth mode of the lignotuber. Chattaway (1958a) similarly observed that lignotubers have a complex anatomical structure and irregular growth mode.

A further factor complicating the interpretation of lignotuber growth rings was tissue damage caused by boring insects and by fungal attack. Tissue damage of this type often obliterated any ring structures, and in some sections had resulted in complete degradation of large sections of wood. Field observations indicated that degradation of the centrally-located wood of lignotubers is a common phenomenon in many mallee populations.

It appears therefore that ring analysis of lignotuber wood does not provide a suitable technique for ageing mallee genets. Ogden (1978) noted similar difficulties for eucalypt stem wood, and concluded: "due to lack of clearly defined annual rings, numerous intra-mural bands ... and the almost total absence of preserved dead wood, the genus Eucalyptus may be of limited potential in dendrochronology".

2.3 Radiocarbon dating

2.3.1 Introduction

A method which has been used with some success in ageing woody plants involves radiocarbon dating of the oldest tissues of the plant. Only one radiocarbon age determination of mallee lignotuber wood has been reported. The lignotuber was described as "suspected to be several thousand years old", but the investigation yielded a 'modern' (<200 years) radiocarbon age (Grant Taylor and Rafter 1963). Measurements of further lignotuber samples were made in order to verify this result.

2.3.2 Methods and Results

Radiocarbon age determinations were made on eight lignotuber wood samples taken from four lignotubers. The methods, testing of the methods, and the results for this investigation have been published (Wellington *et al.* 1979), and a copy of the paper has been included as an appendix (see Appendix 1).

2.3.3 Discussion

The radiocarbon ages obtained for lignotuber wood (see Wellington *et al.* 1979) apparently confirm the previous finding (Grant Taylor and Rafter 1963), and support the observation made by Ogden (1978) that most *Eucalyptus* have life spans of less than 400 years.

Although radiocarbon dating techniques indicate that the age of lignotuber wood is less than 200 years, these techniques are not sensitive enough to detect age differences between samples whose ages fall within 200 years of the 'modern' reference standard (Polach, 1975).

As a result, ages of individual lignotubers cannot be determined by this method. It was therefore concluded that radiocarbon techniques are not suitable for determining the age structure of mallee populations.

It should be noted that radiocarbon age determinations do not finally resolve the problem of whether or not lignotubers may be very old. Age determinations can be made only on extant tissues. It may be possible that tissues older than ca 200 years are completely degraded. Therefore, mallee lignotubers may be able to attain great genetic age, although their apparent age measured from extant tissues is much younger.

2.4 Amino-acid racemization

The study of rates of racemization of amino-acids is a potentially useful technique for determining the age of certain organic and fossil materials (Smith et al. 1978). However, it is evident from the literature that considerable development of the technique is needed before the usefulness this approach can be fully evaluated. Potential difficulties arise from the fact that the stability of racemization rates may be affected by changes in environmental factors, particularly temperature. Development of this technique to the point where it might be used for ageing lignotubers would have required a considerable amount of time. Therefore the technique was regarded as impractical for use in a short-term demographic study.

2.5 Size-class analysis

Measurements of the size distribution of a population may provide considerable insight into its age structure, provided there is a direct relationship between size and age for the particular species under consideration. It is usually necessary to demonstrate a size-age relationship empirically using some independent measure of age for each species, since size has often been found to reflect dominance rather than age (Harper 1977). The absence of a reliable technique for calibrating lignotuber size against age precludes the use of a size-class analysis in a demographic study of mallees.

A further complication arises from the irregular mode of growth of lignotubers (Chattaway 1958a) and their tendency to fragment as necrosis destroys the older tissues. An initial survey of size distributions of a mallee population indicated that accurate size estimates were impossible for many lignotubers due to fragmentation and decay.

2.6 Towards a demographic study of mallee

The investigations described in the previous sections indicated that: mallee genets are long-lived (ca 200 years); mallee populations are likely to have unstable age structures; and that there are presently no suitable techniques for ageing individual lignotubers.

Despite these limitations, it is possible to collect important demographic information for mallee populations. The identification of broad life stage classes (e.g. seed, germinant, seedling, juvenile, adult) is possible for populations of most plant species, including mallee eucalypts. Estimations of the mortality rates of genets in different life stages can be made over relatively short time periods

(two or three years) in all but the most static populations. If the apparent age of mallee lignotubers (ca 200yrs) is a true indication of genet age, then it is likely that mallees are similar to most other eucalypt species in having a life-span in the vicinity of 400 years (Ogden 1978), rather than the previously suspected age of "several thousand years" (Grant Taylor and Rafter 1963). In this case, the movement of genets through different life stages will be rapid, and estimations of the rate at which genets move between successive life stages, particularly during the early part of the life-cycle (ie. seed, germinant, seedling), are also likely to be possible in a short term study. Provided that populations can be located in which the greatest possible number of life stages are represented, then the use of a life stage classification may yield valuable insights into the population dynamics of long-lived perennials such as mallees. A similar approach has been used successfully in demographic studies of perennial herbaceous plants by Rabotnov (1969).

2.7 A model of mallee population dynamics

To provide a conceptual framework around which to formulate a demographic investigation of mallee eucalypts, a general model of the life-cycle of mallees was devised (see Figure 2.1). The model was inspired by Harper's (1977) diagrammatic model of a plant population. It was developed using both preliminary field observations and information available in the literature. The model is artificial in the sense that it compartmentalises what is essentially a continuous, dynamic process. However, it is useful to conceptualize such processes in this manner, both for clarification of ideas, and to enable specific processes to be selected for investigation.

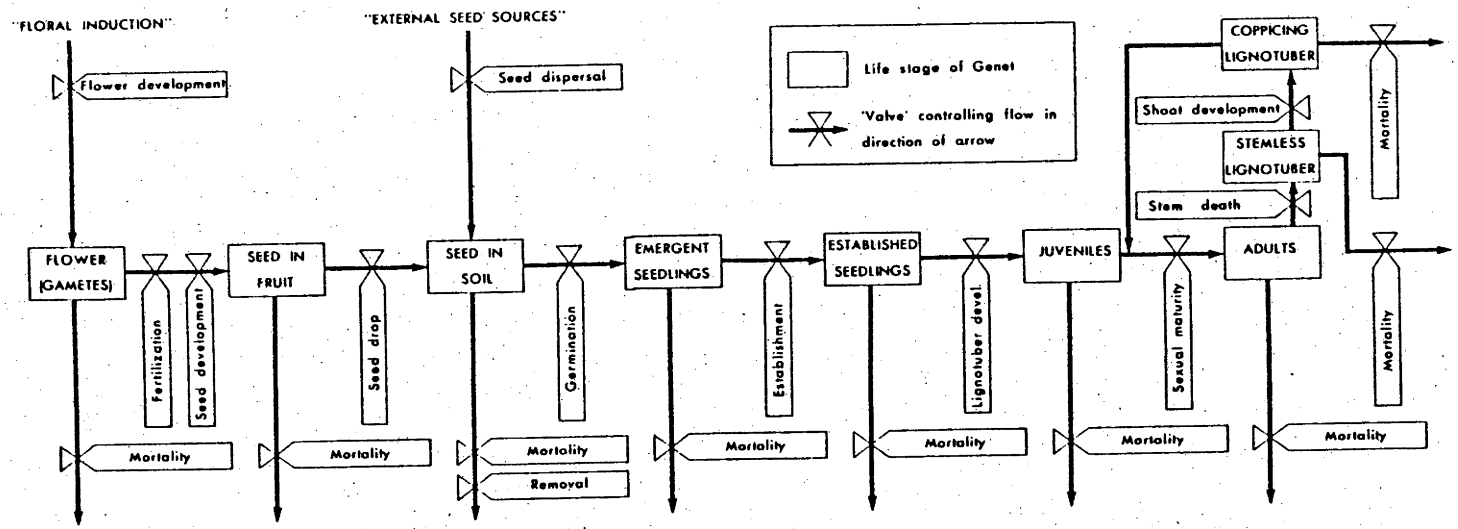


Figure 2.1 A model of mallee population dynamics

The model is based upon the following life stages: flower (gametes), seed, emergent seedling, established seedling, juvenile, and adult. These life stages represent a sequence through which genets must pass to reach maturity.

Each box in Figure 2.1 represents a different life stage. The arrows signify possible directions in which genets can move. Processes controlling genet movement between life stages (e.g. germination, establishment, lignotuber development etc.) are represented as 'valves'. Definitions relevant to the model are included in Table 2.1.

Successful fertilization of gametes results in the production of new genets (i.e. seeds), which enter the sequence of life stages on the left hand side of the model (Figure 2.1). Genets at any particular life stage eventually either move on to the next life stage in the model, or they die. The final life stage (i.e. 'adults') is associated with sexual maturity (i.e. 'flowering'), and the production of new genets via gametogenesis and fertilization.

Mallee populations are subject to recurrent fire (Section 2.1). The effects of fire are represented in the model by the process 'stem death' which results in a 'stemless lignotuber'. The process of 'stem development' produces a 'coppicing lignotuber'. The stems may eventually reach sexual maturity. Other factors may also result in stem death (e.g. disease, physical damage); these factors superimpose a similar cycle on adult mallees. Juveniles also possess a lignotuber. Therefore they respond to stem death in a similar way to adults. The response of juveniles to stem death has not been included in Figure 2.1 for the sake of clarity.

All genets ultimately move out of the model via the process of mortality. Mortality may occur at any life stage in the model.

2.8 A recruitment survey

In order to obtain the maximum amount of demographic information concerning mallee populations in a short term study, it is necessary to have as many life stages as possible present in the population being studied. A search for suitable populations in mallee areas in south-eastern Australia was undertaken over a period of twelve months. Efforts were made to locate sites where recent recruitment had occurred.

Each of the mallee regions examined were found to comprise a mosaic of areas burned at different times. Sites with seedlings were rare. Occasional seedlings were located in recently-cleared areas, and in sites of recent soil disturbance (e.g. roadside clearings, dam sites). These occurrences support the observations made by Sims (1951) and Ioannou (1968) (see Chapter 1).

From a large number of both long-unburnt sites and recently-burnt sites examined, only four sites of widespread recruitment were located. Two of these sites had previously been described in the literature, and included an area burned in 1965 on the property 'Yara', near Mt.Hope, New South Wales (Holland 1969a), and an area at Hattah, Victoria, which was burned in 1972 (George 1974). A third site was located on the property 'Mylatchie' near Balranald, New South Wales, and contained very dense seedling regeneration following a fire in 1967 (R.Parker, c/o "Hazelwood", via Balranald, personal communication). The fourth site was located in the Big Desert to the west of Lake Albacutya, Victoria. This site was burned in December 1977, and extensive germination

occurred in April/May 1980 (P.Cheal, Victorian National Parks Service, personal communication).

Three of the sites were not suitable for a demographic study as at least five years had elapsed since they had been burned, and only the 'juvenile', 'adult' and 'coppicing lignotuber' life stages (see Figure 2.1) were represented. The fourth site, located west of Lake Albacutya, was potentially the most useful since germination was still in progress when the site was first visited (June 1978), and consequently the maximum possible number of life stages were present. Accordingly, this site was selected for a study of mallee population dynamics.

2.9 A demographic study of *E. incrassata*

The site selected for study was found to support populations of several species of mallee eucalypts. The most common species is *Eucalyptus incrassata* ('yellow mallee'). This species is widespread at the burnt site, occurring over a range of topographic sites, including both dunes and swales (see Chapter 3). *E. incrassata* was chosen for investigation for the following reasons: it has a wide distribution; aspects of its biology have been investigated by Parsons (1966) and by Holland (1967); and it has large seeds (1 to 2mm in length) which can be readily distinguished from chaff, and easily relocated when placed on the soil surface.

Both *E. incrassata* Labill. and *E. incrassata* var. *costata* (Behr. & F.Muell. ex Miq., ut sp.) N.T.Burbidge are present at the study site. Willis (1972) noted: "The form of *E. incrassata* most usual on Victorian Mallee sand-hills is var. *costata* ..., distinguished by its larger, more cylindrical fruits ... with definite ribbing in the dried state, and in the more flattened peduncles; however it grades into the

smoother typical form ...". The morphological differences between these two forms of E. incrassata were not always obvious at the study sites and many intermediate forms were found. There were no obvious differences between the two forms either in terms of topographic and spatial distributions, or in terms of function (e.g. phenology, seed storage etc.). For the purposes of the present study therefore, the two forms were regarded as belonging to a single population; both forms are referred to as E. incrassata in this thesis.

The site was first visited in June 1978. At that time, many seedlings were present and germination was still in progress. Some lignotubers had begun to coppice. Adjacent unburnt stands were composed of adults, many of which possessed reserves of mature capsules containing seed. Many adults had immature buds, indicating that a flowering season would probably occur sometime during the study. Of the life stages described in the model in Section 2.7, the following were present at the Albacutya site in June 1978: 'seed in fruit', 'emergent seedlings', 'adults', 'stemless lignotubers', and 'coppicing lignotubers'. Within the duration of the present study, other life stages including 'flowers (gametes)', 'established seedlings' and 'juveniles' were expected to occur.

To obtain demographic information on the population of E. incrassata at Lake Albacutya, the number of genets present at each life stage was estimated, and the movements of these genets either through successive life stages, or out of the population via the process of mortality, were monitored. Detailed investigations of factors contributing to genet mortality at the seedling and juvenile life stages were made. The processes controlling recruitment via seed dynamics and seed germination behaviour were also examined in detail. These investigations are described in succeeding chapters and an attempt is

made to interpret the demographic information in terms of the overall dynamics of the population with the aid of the model described in Section 2.7.

Table 2.1 Definitions relevant to the mallee model (Figure 2.1)

A. Life stages

Flower (gametes)	- a structure, containing mature gametes, in which fertilization can take place
Seed in fruit	- viable seeds contained in mature capsules
Seed in soil	- viable seeds present in or on the soil
Emergent seedlings	- newly germinated seedlings which are still dependent on the seed reserves
Established seedlings	- seedlings which are no longer dependent on the seed reserves, and have not initiated the development of a lignotuber
Juveniles	- plants which have developed a lignotuber, but whose stems have not yet reached sexual maturity
Adults	- plants which possess a lignotuber and which have flowered
Stemless lignotubers	- plants which have had their above-ground parts killed, but which have not yet initiated production of new shoots from the reserve of lignotuberous buds
Coppicing lignotubers	- plants in which previously dormant lignotuberous buds have begun developing to form new stems, but the stems not yet reached sexual maturity

B. Processes

Flower development - the production of fully-formed flowers containing gametes.

Fertilization - the fusion of two haploid gametes to produce a diploid embryo

Seed development - the formation of a mature seed containing a viable embryo

Seed drop - release of seeds from the capsule

Seed dispersal - the movement of seed across large distances which may result in the introduction of genets from other populations

Germination - reactivation of cellular function in the embryo, resulting in growth and emergence of the embryo from the testa

Removal - movement of seeds to places where either successful germination or establishment is impossible (e.g. deep below the soil surface)

Establishment - development to the stage where a seedling no longer relies on seed resources

Lignotuber development - radial growth of stem tissue associated with the first few leaf nodes to form a structure containing both food reserves and dormant buds. (The possession of a lignotuber gives a plant an important regenerative capacity)

Sexual maturity - attainment of the capacity to produce gametes at the initial onset of flower development (q.v.).

Stem death - death of stems due to any cause. (Fire is the most common cause of stem death, but other

factors including insect attack and fungal necrosis may be significant)

Shoot development - growth of previously dormant buds in the lignotuber (Epicormic shoot development also occasionally occurs in mallees)

Mortality - death of a genet; may be caused by a wide range of factors. Mortality is possible at any life stage, although it may tend to occur more frequently at particular life stages

C. Other factors

Floral induction - a process whereby developmental changes at the shoot apices eventually result in the formation of flowers (q.v.) containing gametes. May result in the formation of new genets.

External seed sources - genets belonging to other populations of the same species.

CHAPTER THREE

THE STUDY AREA

CHAPTER 3

THE STUDY AREA

3.1 Location

The area chosen for the present study is located close to the western side of Lake Albacutya (35°45'S, 141°58'E), approximately 20 km north of Rainbow in north-western Victoria. It forms part of the eastern boundary of a large uncleared mallee area known as the "Big Desert", and lies within the recent southern extension to Wyperfeld National Park (Figure 3.1).

Between 21 and 23 December 1977, a fire caused by a lightning strike burned an area of about 4,000 ha, west of Lake Albacutya. Sites used for the present study are located within this burnt area and along its north-western fringes in unburnt mallee. They are distributed both north and west of the trig station G531-107 (35°43'S, 141°55'E; sheet 72226 (Ed.1), Albacutya; 1:100,000 topographic map series R652).

3.2 Climate

3.2.1 The general climate

A discussion of the climatic range encompassed by mallee areas is included in Chapter 1 (Section 1.3.3). Descriptions of the climate of mallee areas in north-west Victoria may be found in Hannay (1965) and Cheal *et al.* (1979).

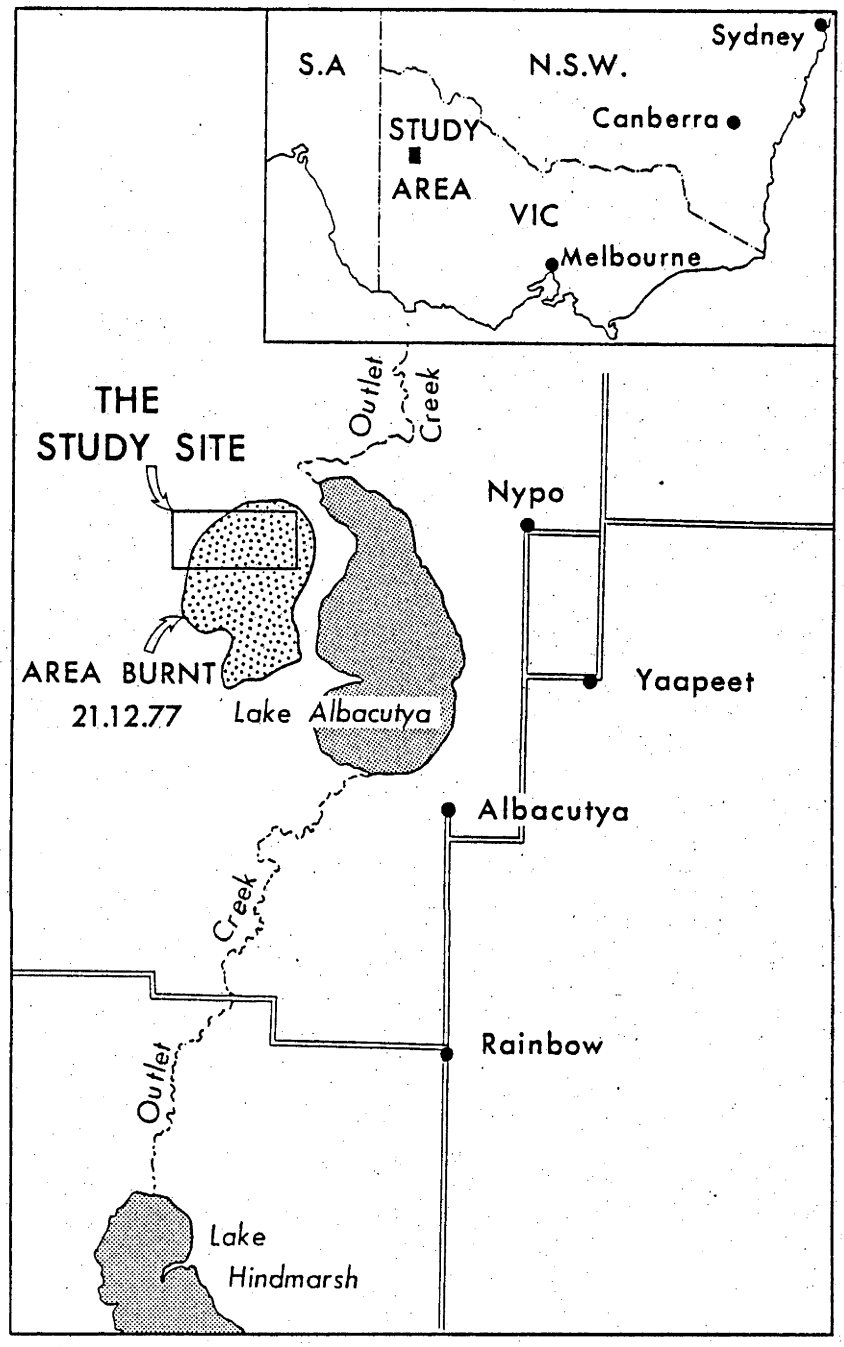


Figure 3.1 Location of the study site

The nearest meteorological station to the study area is 20km south at Rainbow. Climatic records are also kept at Wyperfeld National Park, approximately 15km north of the study site. However these only commenced in 1959 (rainfall) and 1977 (temperature). A summary of climatic averages for Rainbow P.O. (35°54'S, 142°0'E) is included in Table 3.1.

3.2.1.1 Rainfall

Mean annual rainfall for Rainbow over the sixty-nine year period to 1970 was 367mm (Table 3.1). Seasonal distribution of rainfall was almost uniform but with a slight winter maximum; the average six-monthly rainfall total from May to October was 59% of the annual total. The mean number of raindays in summer was much less than in winter indicating heavier falls in summer (mean rainfall per rainday (summer) = 7.4mm; mean rainfall per rainday (winter) = 3.5mm).

Monthly rainfall totals for Wyperfeld National Park for the period 1959-1979 are included in Table 3.2. These demonstrate the high variability that occurs both between months and between years. Summer rainfall is particularly erratic, with very low or zero values commonly occurring in January and February.

Periods of zero rainfall lasting more than twelve months occurred in north-west Victoria in 1895-1902, 1913-1915, 1918-1920, 1925-1930, 1942-1945 and 1966-1968. Shorter droughts are more common, and even in years of average rainfall, dry spells which limit plant growth occur (Land Conservation Council Victoria 1974).

Table 3.1 Meteorological data for Rainbow, Victoria

(Source: Commonwealth Bureau of Meteorology (1975) "Climatic Averages, Australia")

Latitude 35 Deg 54 Min S Longitude 142 Deg 0 Min E Elevation 89.6 M

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
9 am Mean Temperatures (C) and Mean Relative Humidity (%)													
Dry Bulb	22.2	21.3	18.4	14.1	9.9	6.6	6.4	7.8	11.1	15.8	17.7	19.3	14.2
Wet Bulb	15.7	16.0	14.3	11.5	8.5	5.9	5.7	6.7	8.9	11.6	12.6	14.3	11.0
Dew Point	10	12	11	9	7	5	5	5	6	7	8	10	8
Humidity	47	55	61	71	82	90	89	84	73	57	52	55	68
Daily Maximum Temperature (C)													
Mean	32.0	31.3	27.4	23.4	18.1	15.5	14.5	16.4	18.6	24.5	25.8	28.1	23.0
86 Percentile	38.3	38.3	33.3	28.9	22.4	18.3	16.7	19.4	23.3	30.6	32.8	35.0	
14 Percentile	26.1	25.6	22.2	18.3	14.4	12.8	11.7	13.3	14.4	18.2	19.7	22.2	
Daily Minimum Temperature (C)													
Mean	14.3	14.8	12.2	9.4	6.6	4.1	3.7	4.5	5.6	8.1	9.9	11.7	8.7
86 Percentile	19.4	20.2	16.7	12.8	10.6	7.5	6.1	7.2	8.4	12.8	14.4	16.1	
14 Percentile	10.0	10.6	8.3	5.6	3.3	1.1	1.1	1.7	2.3	3.9	5.6	7.8	
Rainfall (mm)													
Mean	20	27	21	25	37	36	37	37	36	35	29	27	367
Median	10	17	14	17	34	35	35	35	32	31	22	20	374
Raindays (No)													
Mean	3	3	3	5	8	9	11	11	9	8	6	4	80

Table 3.2 Rainfall records, Wyperfeld National Park (mm)

Year	J	F	M	A	M	J	J	A	S	O	N	D	Total
1959	0	19.8	39.1	0	8.1	5.1	8.1	20.6	31.0	31.2	8.9	25.7	197.6
1960	56.6	27.9	24.4	51.1	76.5	35.3	38.1	36.6	60.5	3.8	76.7	1.0	488.5
1961	0	11.2	6.6	60.7	13.2	26.2	27.4	32.5	36.3	28.7	7.1	87.9	337.8
1962	76.2	0	13.2	0.8	33.8	25.9	15.2	36.1	28.4	30.0	3.8	45.2	308.6
1963	49.8	0	38.4	50.8	45.0	110.0	45.5	37.8	30.2	22.9	2.8	24.6	457.8
1964	6.6	3.0	0	26.9	20.8	27.9	38.4	40.4	97.8	70.9	49.3	10.7	392.7
1965	0	0	4.3	22.9	23.6	15.2	43.4	52.1	19.8	1.3	42.7	28.2	253.5
1966	20.1	30.5	22.6	8.6	10.7	7.1	37.1	17.5	37.8	30.7	18.3	58.2	299.2
1967	1.5	29.5	1.5	0	14.5	6.6	24.1	28.7	16.8	7.9	1.8	11.4	144.3
1968	18.5	21.8	54.4	34.0	56.1	30.7	18.5	51.3	18.5	34.8	22.1	26.7	387.4
1969	2.8	89.4	79.5	21.6	27.4	11.2	46.7	29.5	23.6	3.0	14.5	22.4	371.6
1970	23.8	1.0	58.4	109.2	14.7	20.3	11.4	37.8	27.7	8.6	55.4	24.9	393.2
1971	2.0	9.9	97.5	52.8	22.9	29.7	21.3	15.7	34.3	20.3	49.3	16.0	371.7
1972	19.8	38.4	0.8	28.4	36.1	7.9	13.7	32.5	16.3	22.6	20.1	3.6	240.2
1973	8.6	111.3	21.8	16.5	55.4	72.4	48.8	55.4	37.3	87.4	49.5	22.9	587.3
1974	86.6	16.5	82.8	94.2	40.4	16.5	31.8	38.1	43.7	70.6	7.9	4.6	533.7
1975	1.8	0.8	18.0	2.5	39.9	7.6	35.8	17.0	47.8	158.2	7.4	27.9	339.7
1976	14.2	45.0	0	19.8	10.4	17.3	25.1	15.2	30.2	63.8	61.0	11.4	313.4
1977	14.0	11.0	13.5	16.3	37.5	18.5	8.5	13.3	12.3	17.8	22.0	18.5	203.2
1978	10.3	1.3	49.5	14.3	61.5	31.8	81.3	53.0	63.3	30.8	69.0	12.5	478.6
1979	83.3	48.8	18.0	17.8	48.3	22.0	10.0	41.0	69.0	42.5	49.8	0.5	451.0

3.2.1.2 Evaporation

Evaporation data for Ouyen (35°4'S, 142°19'E), approximately 80km north-west of the study, was obtained from Cheal et al. (1979). Average annual evaporation at Ouyen is 1340mm, and ranges from a summer monthly average of 206mm to a winter monthly average of 45mm. The high evaporative loss in summer greatly reduces the effectiveness of summer rainfall. Evaporation rates for Rainbow are likely to be similar to those for Ouyen.

3.2.1.3 Temperature

Temperature variations at Rainbow are fairly wide, the mean monthly maximum and minimum varying from 31°C and 15°C in February to 15°C and 4°C in July (Table 3.1). Temperature extremes in summer may exceed 40°C, and in winter there is a frost incidence of 5-15 days per year (Cheal et al. 1979).

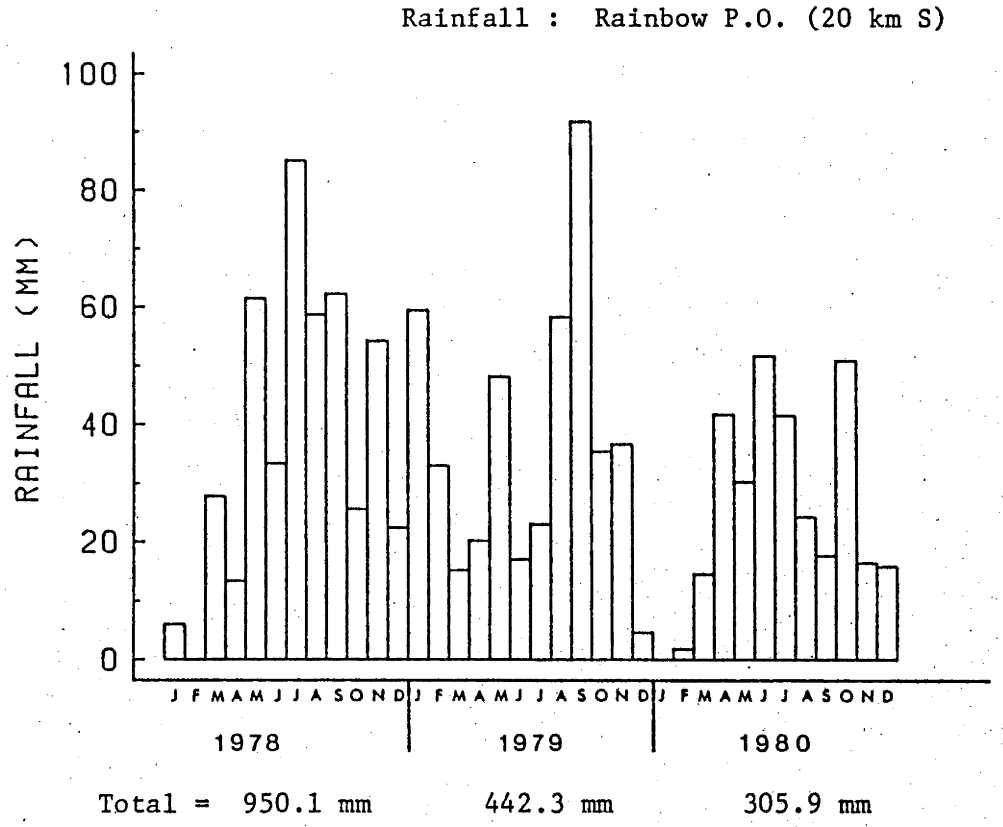
3.2.1.4 Winds

Prevailing winds in the north-west of Victoria are from the south-west, west and north-west. Seasonal variations are slight. Wind speeds of between 5 and 10 knots are common, but wind speeds may reach gale force on several days each year (Land Conservation Council Victoria 1974).

3.2.2 Climate at the study sites: 1978-1980

3.2.2.1 Rainfall

Monthly rainfall totals for the period 1978-1980, measured at Rainbow P.O., and at a local property (R.E. Goslings's, via Yaapeet) located approximately 7km north-east of the study area, are plotted in



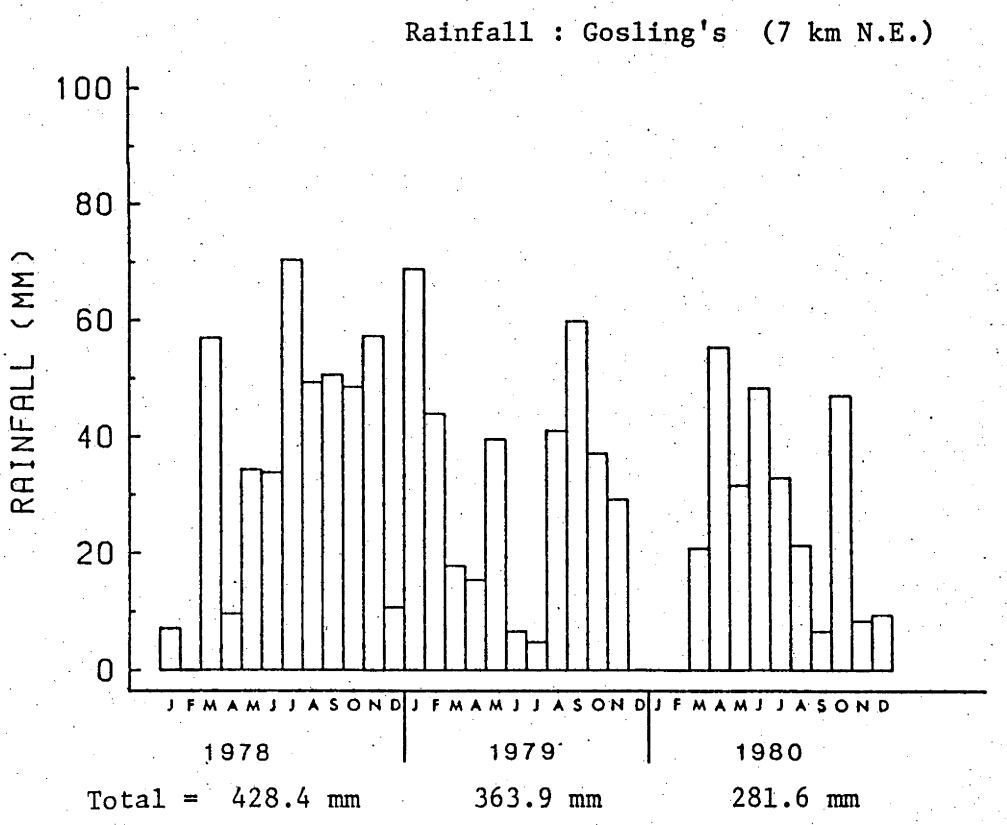


Figure 3.2 Monthly rainfall totals (1978-1980)

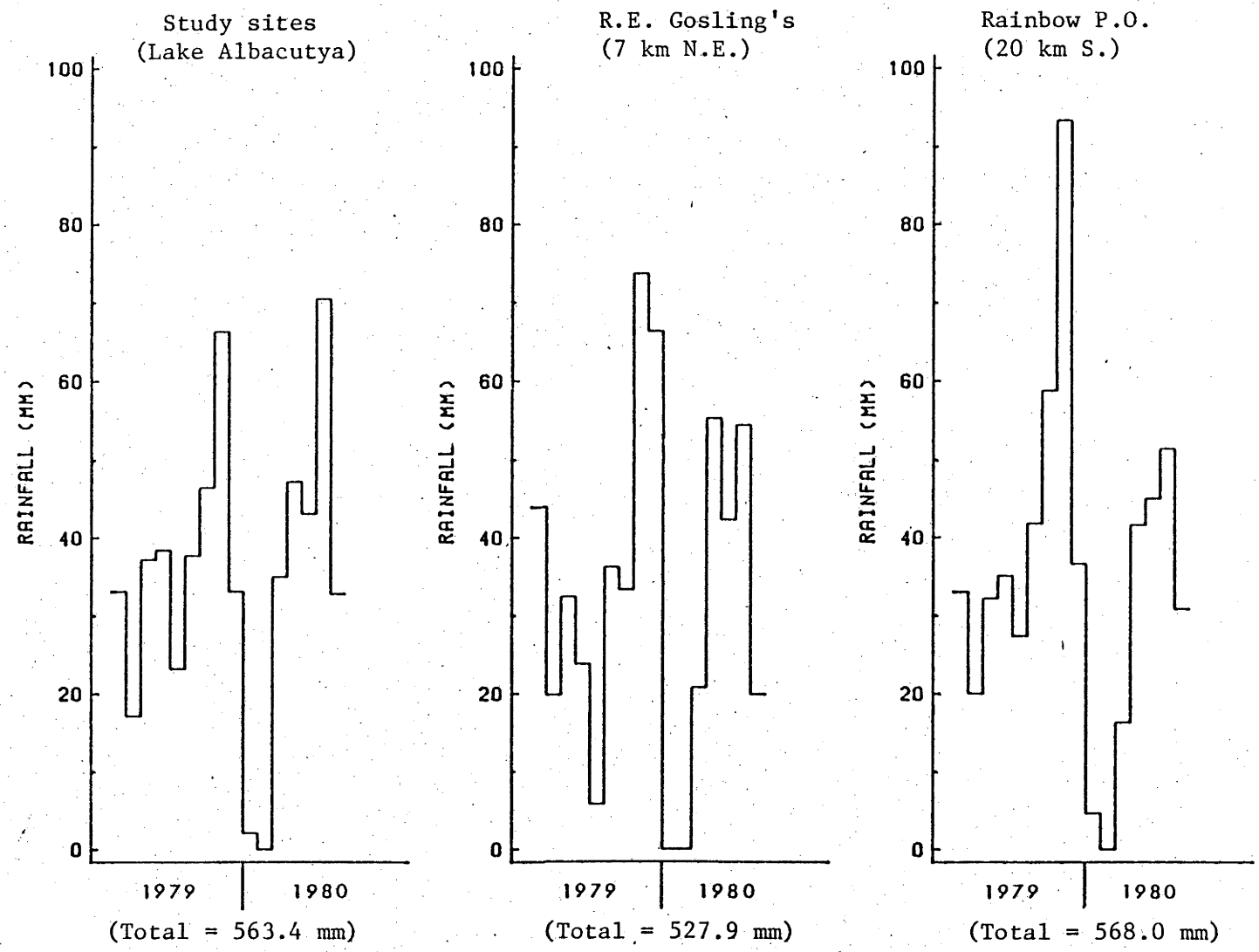


Figure 3.3 Rainfall totals between field trips (1978-1980)

Figure 3.2. These demonstrate the spatial variability of rainfall in the region. Heavy localized thunderstorms are common, and account for much of this variability.

At the study area, five-inch diameter metal raingauges were set up at nine sites on 23 January 1979. These were distributed so as to encompass the topographic variation of the area and were situated along a N.E.-S.W. line of about 4km length which traversed the study area. Approximately 0.3 litres of liquid paraffin was added to each raingauge to minimise water loss due to evaporation. The contents of the raingauges were measured during each field trip over the period from 23 January 1979 to 16 August 1980.

Rainfall totals between field trips, expressed as the mean total for the nine raingauges at the study area are plotted in Figure 3.3. Rainfall totals for the same time intervals for both R.E. Gosling's property (7km N.E.) and Rainbow P.O. (20km S.) are plotted alongside. These further demonstrate the high spatial variability of rainfall in the area.

Variability of rainfall across the study sites was slight. Raingauges at similar elevations, but separated by up to 4km, showed similar rainfall totals for the nineteen months of measurement. However some variation in rainfall occurred between paired rainguages in swales and on crests (Table 3.3).

Table 3.3 Variation of rainfall totals with site elevation.

Vertical separation (m)	Horizontal separation (m)	Swale total (mm)	Crest total (mm)	Rainfall difference (mm)
10	170	575.0	564.6	11.0
18	150	579.6	556.5	23.1
19	130	568.0	559.2	8.8
44	370	579.6	520.3	59.3

More elevated sites experienced a slightly lower rainfall total when compared to adjacent swale sites. A similar effect has been noted by Rayson (1957) for sand dunes in the Ninety-mile Plain, S.A. Rainfall variation on dune slopes of different aspect was also shown to differ slightly. This was not investigated in the present study.

3.2.2.2 Air Temperature

Two Stevenson screens were set up to enable measurement of air temperatures and relative humidity. One was located on the crest of a broad, high dune in the northern part of the burnt area and the other was installed in a low-lying swale approximately 0.5km further south. Each weather screen was equipped with a maximum-minimum thermometer and a weekly thermohygrograph (Sato Keiryoki Co., catalogue no. 307). The vertical distance between the two weather screens was approximately 15m. The swale screen was installed on 6 May 1979 and the dune crest screen was installed on 3 November 1979. Measurements using both screens were continued until 28 July 1980.

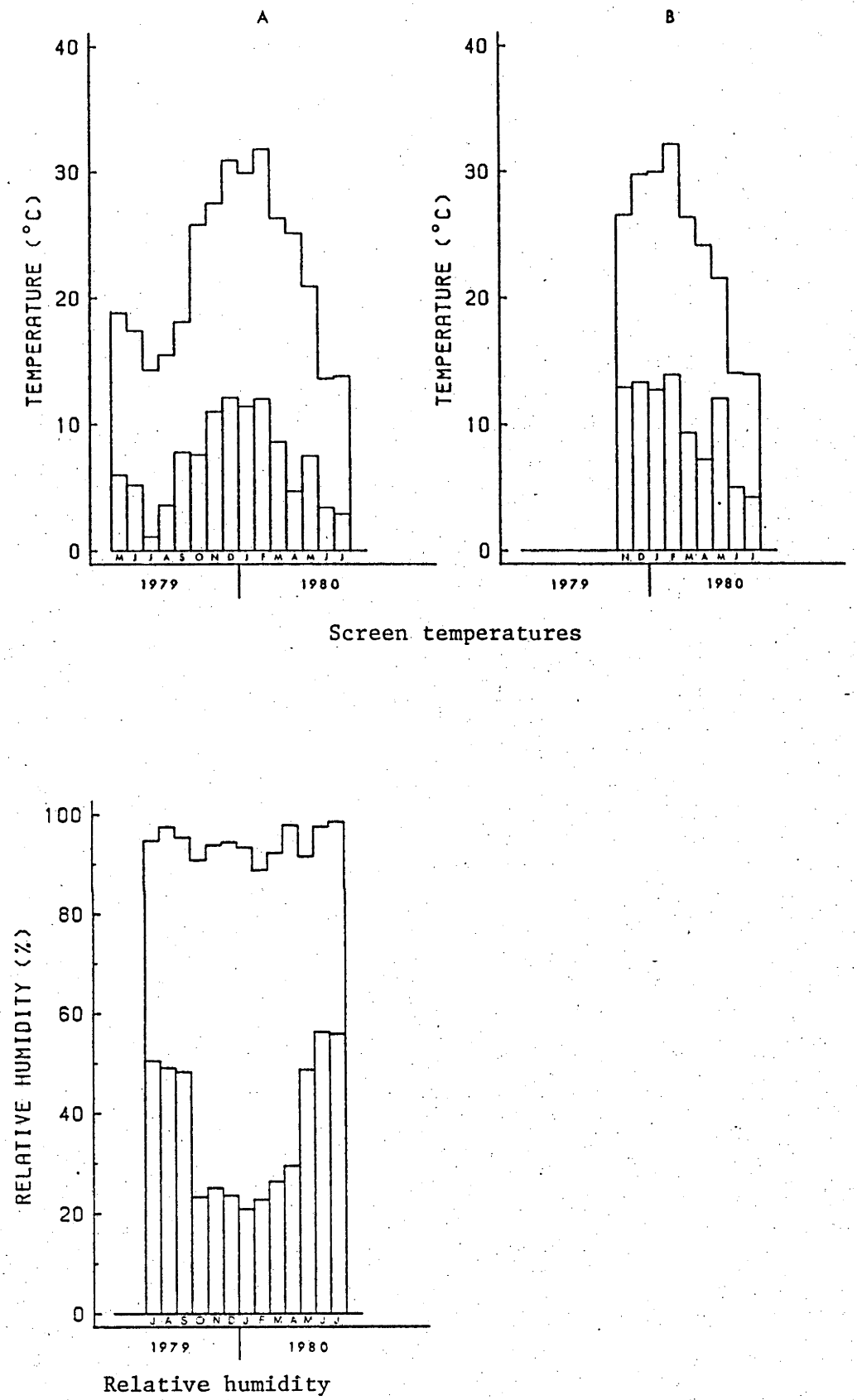


Figure 3.4 Mean monthly maximum and minimum screen temperatures for a swale (A) and a dune crest (B), and mean monthly maximum and minimum relative humidities for the swale (A) at the field sites west of Lake Albacutya. (Elevation difference = 15 m)

Maximum recording time for a thermohygrograph was two weeks. Records from each thermohygrograph were obtained for the duration of each field trip plus an extra two weeks between each trip. Mean monthly maximum and minimum temperatures and the number of recording days in each month are plotted in Figure 3.4. Maximum temperatures were similar between the two sites. Minimum temperatures at the swale site were consistently 2-3°C lower than those measured at the dune crest site. This was probably due to cold air drainage into low-lying sites during the night.

3.2.2.3 Relative Humidity

Relative humidity was monitored from 21 July 1979 to 28 July 1980. There was little difference in relative humidity between the crest and swale sites during the periods of measurement. Mean monthly maximum and minimum relative humidity values for the swale site are plotted in Figure 3.4.

3.3 Vegetation

A comprehensive description of the flora of north-west Victoria may be found in Zimmer (1946). General descriptions of similar vegetation types in New South Wales (Beadle 1948), and South Australia (Specht 1972) also provide useful information. Recent floristic analyses of mallee communities in north-west Victoria have been carried out by Noy-Meir (1971) and Cheal *et al.* (1979).

The vegetation at the study sites is largely dominated by mallee eucalypts, interspersed with occasional stands of heath and *Callitris*. The most common mallee is *Eucalyptus incrassata* which occurs on the

dunes and in the smaller swales. Most of the components of the Eucalyptus incrassata - Glischrocaryon behrii association described by Cheal et al. (1979), occur in the area. The larger swales support communities dominated by E. dumosa, E. foecunda and E. calycogona, and include elements of the Eucalyptus foecunda - Senecio quadridentatus, the Eucalyptus calycogona - Pterostylis mutica and the Eucalyptus dumosa - Senecio lautus associations of Cheal et al.(1979). The higher dune ridges often support a Casuarina muellerana - Leucopogon cordifolius association with elements of the heath communities characterized by Leptospermum coriaceum and Aotus ericoides.

3.4 Geology, Geomorphology

A detailed geological description of the mallee areas of Victoria may be found in Lawrence (1966). Discussions of the geomorphological development of the region are given by Hills (1939), Rowan and Downes (1963), Gill (1966), and Bowler and Magee (1978).

The study area consists of a quaternary aeolian deposit, known as the Lowan Sand, overlying Tertiary sands and limestone formations. The Lowan Sand is a greyish-yellow, fine to medium-grained siliceous sand derived from underlying Tertiary sediments. This deposit is of varying thickness and forms irregular wind-blown dunes separated by swales and occasional extensive sand plains (Lawrence 1966).

Dune systems close to Lake Albacutya are mostly irregular, and include parabolic and sub-parabolic forms. They are of varying height and sometimes exceed 30m; occasional dune hummocks occur. The swales are of greatly varying size and elevation. Further west, linear dunes and extensive sand plains are common (see Rowan and Downes 1963).

3.5 Soils

The dune soils of the study area are predominantly deep siliceous sands of low fertility and little profile development. Soils of low-lying areas, particularly in the larger swales, show some profile development and resemble the "solonized brown soils" described by Stace et al. (1968). These are medium-textured calcareous soils and range from sandy loams to sandy clays. Occasionally, "solonetz" soils, which exhibit an abrupt change from a sandy loam to a sandy clay in the profile, are found in the swales.

In general, the nutrient status of mallee soils increases with increasing clay content (Land Conservation Council Victoria 1974) Swale soils therefore tend to have a higher nutrient status than the deep sands of the dunes.

3.6 Soil Moisture

3.6.1 Methods

Samples for soil moisture determinations were collected from three different sites, viz: a dune crest, midslope and in the adjacent swale. The loose substrate on the dunes necessitated the use of soil pits for sampling; a soil auger was used in the swales. Samples were collected from the following depths: 0, 0.1, 0.2, 0.4, 0.6, 0.8, 1.0m. One pit was dug at each site on each collecting day, but samples were taken from four different points within the pit at each depth. The samples for each depth were bulked, sealed in plastic and stored at low temperatures (<15°C).

Soil moisture contents were determined gravimetrically using the method of Gardner (1965) in Black et al. (1965; pp 92-96). Determinations of soil moisture were made in duplicate. Soil bulk densities and field capacities were determined according to Blake (1965) and Peters (1965) respectively, both in Black et al. (1965; pp 375-377 and p 281). Soil moisture content, determined as percent water per unit oven-dry weight, was recalculated using bulk density estimations as percent water per unit volume.

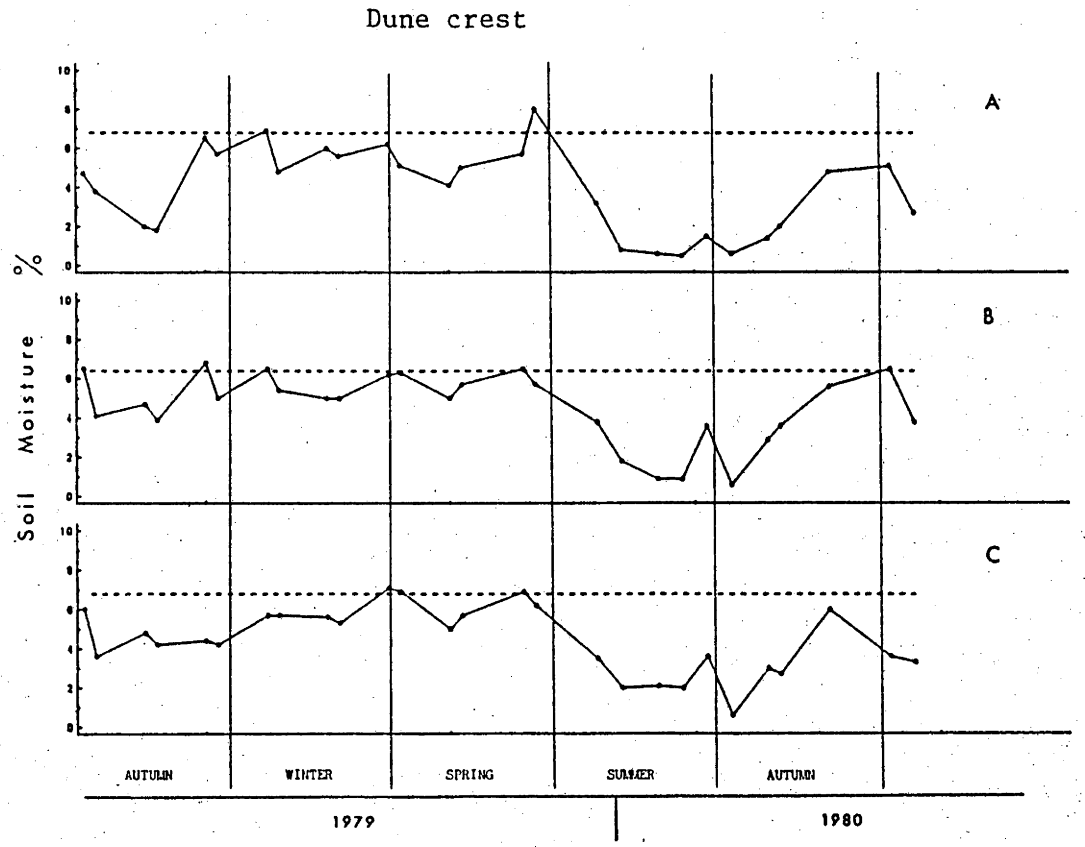
Samples were collected at the beginning and at the end of each field trip during the period March 1979 to June 1980. The same general localities were used each time. Two raingauges were installed in the vicinity of the sampling areas (see Section 3.2.2.1), and rainfall totals between field trips were determined. Intervals between field trips varied from two to five weeks. A total of twenty-seven collections were made spanning a period of seventy weeks.

3.6.2 Results and discussion

To simplify data presentation, mean soil moisture values were calculated for the following depth intervals: 0.1-0.2m; 0.2-0.6m; 0.6-1.0m. Surface samples were not included.

Soil moisture data for the three sites (i.e. crest, dune slope and swale) are presented in Figures 3.5a and 3.5b. Rainfall totals between field trips, expressed as a mean of the two raingauge totals, are also included in Figure 3.5b.

Soils at the two dune sites consisted of deep siliceous sands with no profile development to 1.0m. The swale soil belonged to the 'solonetz' classification of Stace et al.(1968) (see Section 3.5) and



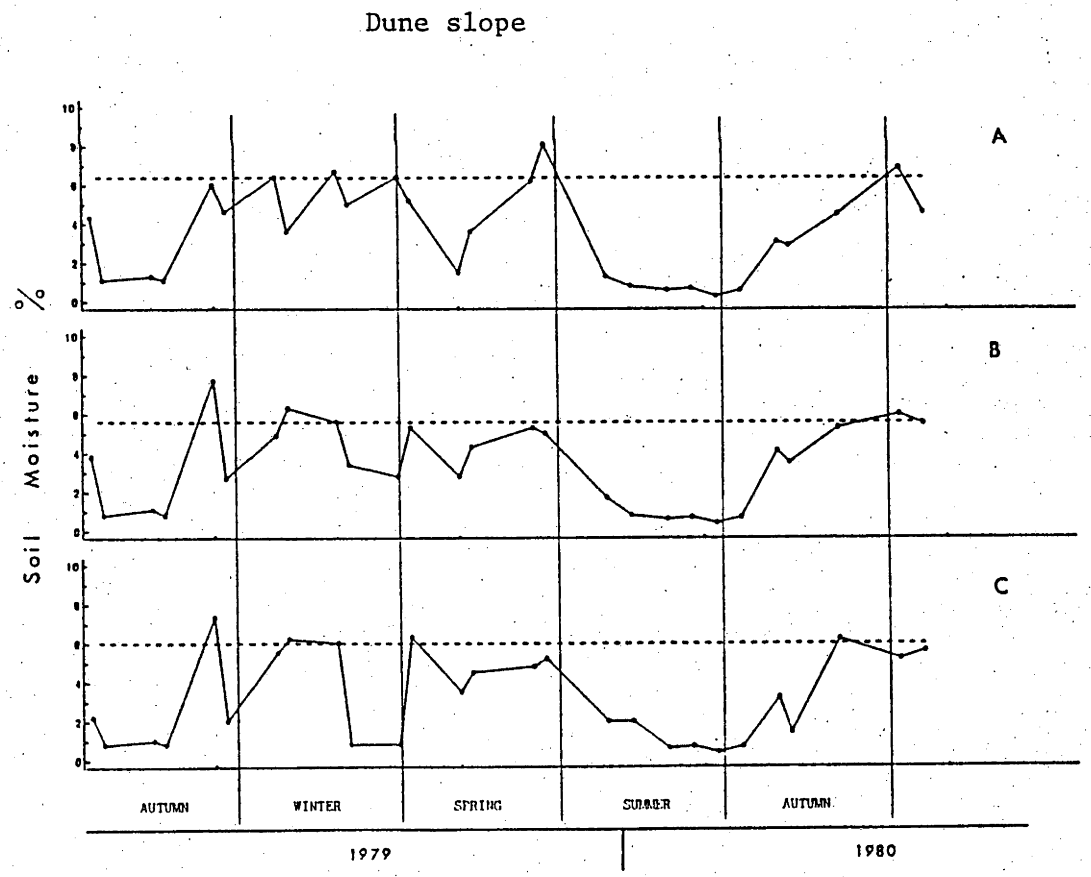
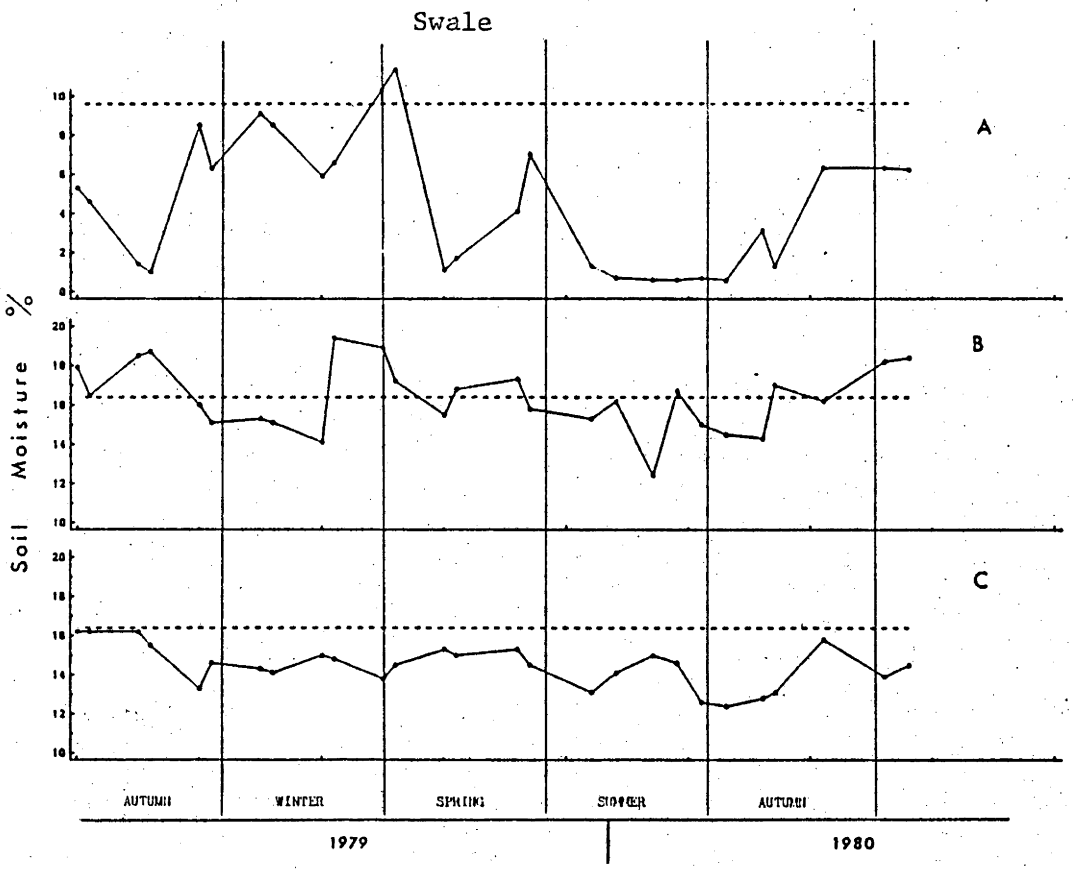
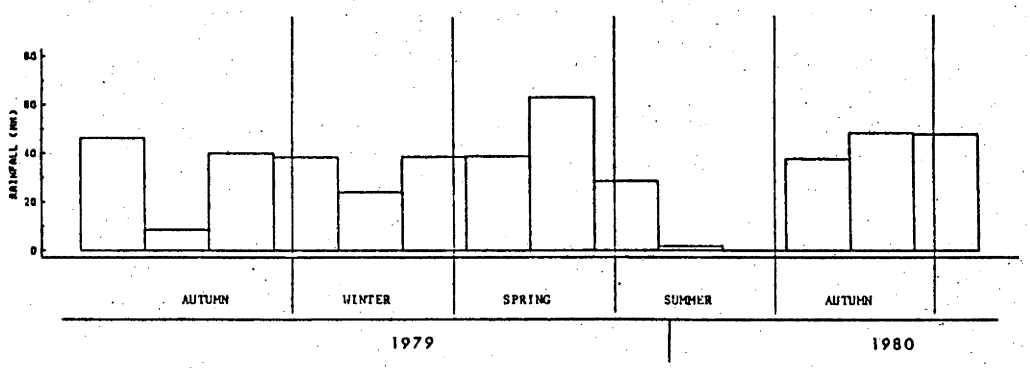


Figure 3.5a Soil moisture (% of soil volume)



Soil moisture (% of soil volume)

Depths: A = 0.1 - 0.2 m
B = 0.2 - 0.6 m
C = 0.6 - 1.0 m



Rainfall totals between soil moisture sampling times

Figure 3.5b

comprised 0.2-0.3m of siliceous sand with a high humus content in the A1 horizon overlying a hard pan of sandy clay with a high carbonate content.

The soil moisture data for the dune sites (Figure 3.5a) indicate a high moisture content during winter and spring of 1979 and a greatly reduced moisture content during summer and early autumn of 1980. The broad trends in soil moisture appear to follow the rainfall pattern (see Figures 3.5b and 3.2); this is most evident for the upper 0.2m of the soil profile. Close relationships between rainfall and soil moisture storage have been demonstrated for similar soils on dunes in South Australia (Rayson 1957, Specht and Rayson 1957a).

An important factor influencing soil moisture distribution is heterogeneity of the soil environment. Variations of soil moisture within one locality may reflect not only the spatial heterogeneity of soil factors such as soil wettability but may also be influenced by the overlying vegetation (Specht 1957a). The problem of sampling a heterogeneous soil may be partly overcome by taking large numbers of replicate samples. In the present study, however, time limitations meant that only one soil pit could be dug at each site on each sampling day. The variability within seasons, evident in the soil moisture profiles (Figures 3.5a and 3.5b), therefore reflects both temporal changes due to the rainfall pattern and spatial changes due to soil heterogeneity. The vegetation at the sampling sites had been recently burnt (in December 1977) and consequently its influence on soil moisture patterns during 1979 and 1980 was likely to be small due to the dramatic decrease in leaf area following the fire.

The upper 0.2m of the swale soil was similar in texture to the dune soils but showed greater variability of soil moisture content within seasons. Possible factors influencing this increased variability include water runoff from the dune slopes into swales, and impeded drainage due to both topographic factors and the underlying clay horizons. Soil moisture changes between seasons for these upper horizons broadly follow the rainfall pattern (Figures 3.5b and 3.2). The lower horizons of the swale soil exhibited a relatively constant soil moisture content compared with the dune soils. Some within-season variability is evident and there was a slight decrease in soil moisture content during summer.

The soil moisture data for the swale site (Figure 3.5b) reflect the abrupt textural change at 0.2-0.3m depth. Those parts of the profile below 0.2m demonstrated higher soil moisture contents and an increased field capacity with respect to the upper horizons. These increases were probably due to an increase in clay content in the lower horizons (see Leeper 1967, chapter VI), but may also have been influenced by impeded drainage (see Peters (1965) in Black et al. (1965), p 280). The higher field capacity of the sandy upper horizons of the swale soil with respect to the dune soils was probably also influenced by impeded drainage.

The field capacity of a sandy soil from the Ninety-mile Plain, South Australia, has been determined at 5.5% to 6.5% (Specht 1957b). Holland (1968a) noted that dune soils in Wyperfeld National Park, approximately 20km north of the study site at Lake Albacutya, are similar to the Winkie sands of South Australia, which have an estimated field capacity of 6.2% (Leeper 1967, Table 12, p 67). Heavier loam soils from near Koonamore Reserve in South Australia are described as having field capacities of 16% to 23% (Noble and Crisp 1980). These

values are similar to the estimated field capacities of the two soil types investigated in the present study (see Figures 3.5a and 3.5b).

The higher soil moisture content of the lower horizons of the swale soil may not reflect the availability of soil moisture to plants. The force with which water is held in a soil matrix is inversely related to the pore size of the matrix (Leeper 1967), and soils with a high clay content generally have smaller pore sizes than sandy soils. Soil moisture - pF curves have been constructed for a soil with an abrupt change from a sandy A horizon to a sandy clay in the B horizon (Specht 1957b). The soil investigated showed a moisture content of about 7% at permanent wilting point (pF 4.2) for the sandy clay horizon whereas permanent wilting points for the A1 and A2 horizons occurred at 1.2% and 0.7% soil moisture content respectively. The heavier textured B horizon had less water available than the sandy A horizons, even though it had a higher water content. Similar results for different soil types have been presented by Leeper (1967; Table 12, p 67), and indicate that a sand with 6% water content is effectively as wet as a clay with 32% water content.

Although the relationships between pF and soil moisture content were not investigated in the present study, it is likely that the higher water content of the lower horizons in the swale soil does not reflect an increased availability of soil water to plants. The low soil moisture contents measured for dune soils during summer 1979/80 fall below the permanent wilting point measured for sandy soils by Specht (1957b). It is likely that the swale soils reached similarly low levels of water availability.

3.7 Plant Growth

Calculation of the growing season for Rainbow, Victoria, derived from climatic averages and calculated for dense ground cover, indicates that soil moisture levels adequate for plant growth in this region generally occur between May and October (Land Conservation Council Victoria 1974). Holland (1968a) noted that maximum growth of field layer plants in Wyperfeld National Park (approximately 35km north of Rainbow) occurs between July and December. However he found that the mallee eucalypts in this region attained maximum growth during the dry months from December to April. It would seem that the native perennial species are able to tap deep water supplies and are not as dependent on surface soil moisture as are the field layer species.

Measurements of soil moisture content at the study sites in 1979 and 1980 (Section 3.6) were confined to the upper 1.0m of soil, for practical reasons. The low levels of soil moisture in the upper 1.0m of soil, evident during summer 1979/80 (Figures 3.5a and 3.5 b), were almost certainly below the permanent wilting point (pF 4.2) (Leeper 1967) and would have affected the growth of plants with shallow root systems. A similar phenomenon has been observed in heath vegetation by Specht (1957b) and Specht and Rayson (1957b). Observations during the present study indicated that both coppicing lignotubers and mature adults were actively growing during this dry period, which supports Holland's (1968a) observation.

It is probable that only extreme drought situations, in which deep soil moisture reserves are depleted, affect the growth of the deeper-rooted perennials of these areas. Both shallow-rooted species, and seedlings of the deep-rooted species, are likely to be strongly influenced by rainfall and the depletion of surface soil moisture due to summer evapotranspiration.

CHAPTER FOUR

RECRUITMENT AND SURVIVORSHIP

CHAPTER 4

RECRUITMENT AND SURVIVORSHIP

4.1 Introduction

The few demographic studies that have been made on perennial plants suggest that these species have a high initial mortality rate which declines rapidly with increasing age. Mortality rates over the greater part of the life-span of perennial plants are low and relatively constant. This type of survivorship behaviour has been described using a power function model ($y = y_o x^{-b}$) (Hett and Loucks 1971), and results in a "positively skew rectangular" survivorship distribution also known as a "Type III" survivorship curve (Pearl and Miner 1935, Deevey 1947).

Conventional approaches to the study of survivorship in populations are described in Sections 2.1 and 2.2. In the present study, an approach which involved monitoring the survivorship of individuals in broad 'life stage' classes over a short time-period was adopted (see Section 2.7).

This chapter describes:-

1. an investigation of the initial rates of seedling recruitment which occurred following the December 1977 fire;
2. an investigation of rates of genet mortality between 1978 and 1980, including:
   (a) 'seedling' mortality;
   (b) 'juvenile' mortality;
   (c) 'stemless lignotuber'/'coppicing lignotuber' mortality;
   (d) 'adult' (long unburnt) mortality;

3. investigations of the main environmental factors contributing to seedling mortality and juvenile mortality.

4.2 Recruitment

4.2.1 Introduction

In order to obtain an estimate of the initial rates of seedling recruitment following the Decembr 1977 fire, a broad scale survey of the number of seedlings present in September 1978 was carried out.

Germination commenced at the study sites in April/May 1978, and continued until August/September 1978. During this period, new genets were present at the study site as both 'emergent seedlings' and 'established seedlings' (Figure 2.1). Since germination and establishment during 1978 occurred over a period of several months, and field work was necessarily intermittent, the life stages of 'emergent seedlings' and of 'established seedlings' were included as a single life stage called 'seedlings'. The estimates described in the present section refer to this composite 'seedling' life stage.

4.2.2 Methods

Broad scale estimates of seedling recruitment were obtained using two linear transects subdivided into 1611 contiguous $1m^2$ quadrats and located in the northern section of the burnt area. The transects were parallel, separated by about 500m, and oriented at a compass bearing of 180°. Species and numbers of eucalypt seedlings were recorded for each

quadrat. The transects were recorded in September 1978, by which time most germination had already occurred (see Section 4.3).

4.2.3 Results and discussion

A summary of the recruitment survey data obtained from the transects is included in Table 4.1.

Table 4.1 Summary of recruitment survey transects (September 1978, total area sampled = 1611 m^2).

Seedling type	Number of quadrats with seedl's	% quadrats with seedl's present	No. of seedl's in transect	Mean seedling density (m^{-2}) (quadrats with seedl's present)	Mean seedling density (m^{-2}) (all quadrats)
E.incr.	293	18	1142	3.9	0.7
all euc. species	375	23	1626	4.3	1.0

Seedlings of five species of Eucalyptus including E. incrassata were found in the transect area: the total recruitment rate for the five species was estimated at 1.0×10^4 seedlings per hectare. The recruitment rate of E. incrassata seedlings was estimated at 0.7×10^4 seedlings per hectare.

The frequency distribution of E. incrassata seedling densities are plotted in Figure 4.1. To simplify presentation, only densities of < 20 seedlings m^{-2} are shown on Figure 4.1; the density range depicted includes 81.5% of E. incrassata seedlings in the transects. Seedling densities were generally low, with 44% of E. incrassata seedlings occurring at densities of < 5 seedlings per $1m^2$ quadrat.

Germination at the study sites probably commenced following heavy rains in May 1978 (Section 3.2.2.1), and continued during the period June 1978 to August 1978 (see Figure 4.3a). Survivorship data from quadrats established in June 1978 demonstrate that some seedling mortality occurred between the monitoring periods in August 1978 and October 1978. The recruitment estimates made in September 1978 must therefore be regarded as 'minimum' rates, since it is likely that some seedling mortality had occurred before the time of the measurement.

The results in this section indicate that minimum recruitment rates of E. incrassata at the study sites following the December 1978 fire were ca 10^4 seedlings ha^{-1}.

4.3 Mortality of seedlings and juveniles

4.3.1 Introduction

Knowledge of mortality rates at different life stages is crucial in determining the particular survivorship distribution which characterizes a population. Mortality rates of the early life stages in the mallee life-cycle were investigated by monitoring a large number of genets located in permanent quadrats. This section describes the results of these investigations.

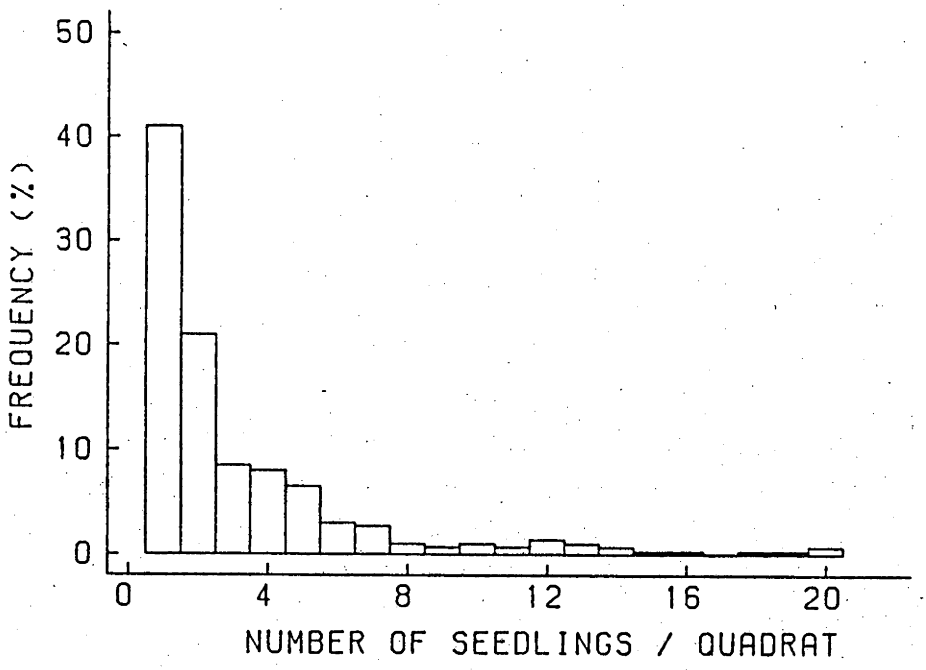


Figure 4.1 Frequency distribution of E. incrassata seedling densities measured in transects in September 1978 (expressed as a percentage of 293 quadrats containing E. incrassata seedlings).

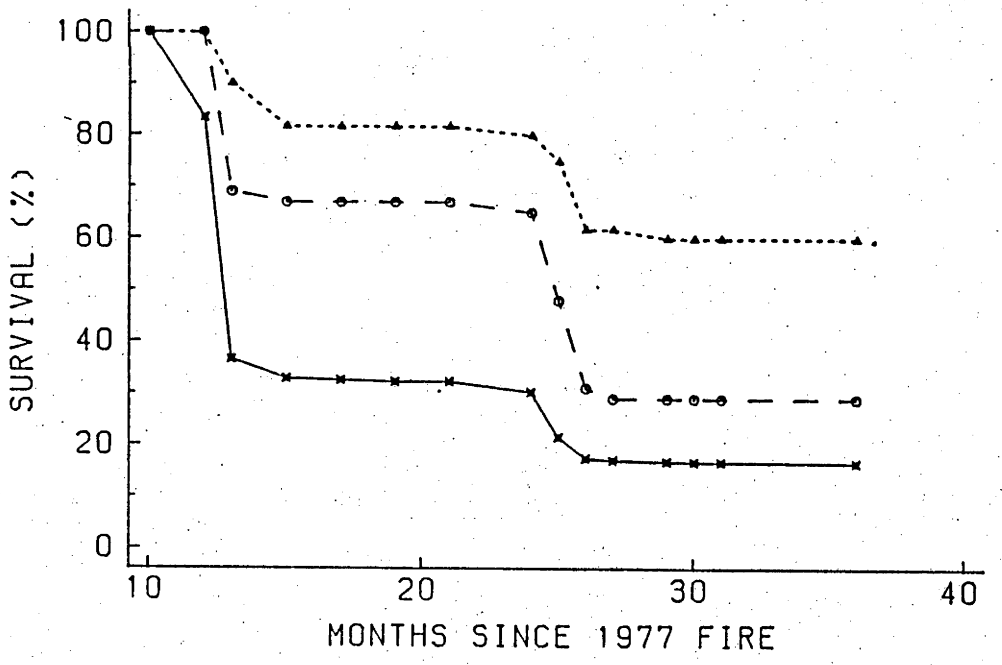


Figure 4.2 Survivorship of new genets in quadrats of three different initial genet densities:
High ($\geq$ 20 genets per m^2) - solid line.
Medium (6 to 19 genets per m^2) - dashed line.
Low ($\leq$ 5 genets per m^2) - dotted line.
(October 1978 to December 1980)

Field work at the study site commenced in June 1978. The first signs of lignotuber development were evident in late 1978, but these were confined to a small number of individuals. By late 1979, the majority of new genets had developed lignotuberous swellings. Therefore, over the period from June 1978 to June 1979, genets were classified as 'seedlings', and from June 1979 to June 1980, they were classified as 'juveniles' (see Figure 2.1). Mortality estimates described in the present section were made during these two periods.

4.3.2 Methods

A total of fifty-one $1m^2$ quadrats were marked out in the northern section of the burnt area. Quadrat sites were selected to cover the range of seedling densities, and to include the major topographic divisions of the dunes, viz: upper slopes (USL), lower slopes (LSL), and interdune areas, or swales (SW).

Seedling densities (D) were divided into three categories, viz: high density (D>20 seedlings m^{-2}), medium density (5<D<20 seedlings m-2) and low density (D<5 seedlings m^{-2}) in order to investigate the effects of density on seedling mortality. Areas of natural recruitment having seedling densities in each of these categories were selected as quadrat sites. The distribution of quadrats amongst the three density categories (Table 4.3) was biased towards higher densities in order to provide sufficient replicates to measure density-dependent mortality.

Each quadrat was permanently marked. In order to monitor survivorship, a $1m^2$ metal frame subdivided into sixteen 0.25 x 0.25 m sections, was placed over the quadrat area and the number of surviving seedlings within each section was recorded.

Monitoring of high-density quadrats commenced in June 1978, medium and low density quadrats in October 1978, and additional medium density quadrats in January 1979. All quadrats were monitored at varying intervals of between one and two months until July 1980.

The transects used for measuring initial rates of seedling recruitment (Section 4.2) were relocated as accurately as possible in August 1980 and the number of surviving seedlings located along the transect lines was recorded. Although great care was taken in relocating the original transect lines, it was not possible to relocate exactly the original $1m^2$ quadrats. Therefore an estimate of total mortality for seedlings in the transects was possible, but comparisons of individual quadrats could not be made.

Mortality data were analyzed to determine differences in mortality rates at the different topographic sites, and at different seedling densities. The G-test of independence for multiway tables (Sokal and Rohlf 1969; pp601-607) was used for the analyses. The convention for representing probability ranges as described by Sokal and Rohlf (1969; p169) is used in this thesis (i.e. * = .05>P>.01, ** = .01>P>.001, *** = P<.001).

4.3.3 Results and discussion

The total mortality of genets (seedlings and juveniles) in quadrats monitored over the period 1978 to 1980 was 80.3% (Table 4.2). A comparison of this figure with the mortality estimates based on the 1978 and 1980 transect measurements indicated that genet mortality in the monitored quadrats was significantly higher ($G_{(1)}$ = 12.530***). This result is likely to have been influenced by the bias towards higher seedling densities used in selecting quadrat sites. The estimates

obtained from the transects were therefore regarded as a more reliable representation of mortality of new genets over the entire site (ca 75% in two years).

Table 4.2 Mortality of seedlings and juveniles (1978 to 1980)

Monitoring method	Species	No. of genets seedlings (1978)	(1979)	juveniles (1980)	%mortality seedl.	juvenile	new genet
Quadrats	E.incr.	1165	415	229	64.4	44.8	80.3
Transects	E.incr.	1142	-	291	-	-	74.5
Transects	All euc.	1626	-	412	-	-	74.7

Survivorship curves for the three density classes are presented in Figure 4.2. Trends in the three survivorship curves were similar, with high mortality confined to the summer months. Table 4.3 summarizes percentage mortalities for genets in each density class of three topographic positions, during the periods from 1978 to 1979 (seedlings), and 1979 to 1980 (juveniles). Medium density data was not collected for all topographic categories, and some measurements were commenced only after the 1978/1979 summer. The following analysis therefore includes mortality data for the high and low density classes only.

Table 4.3 Mortality of seedlings and juveniles at three densities and three topographic positions (1978-80)

Seedling density	Position on dune	Number of quadrats	Number of seedlings at commencement	Seedling mortality (%) (to June 1979)	Number of juveniles (June 1979)	Juvenile Mortality (%) (June 1979 to June 1980)
High	Upper	6	408	88	49	71
	Lower	4	194	37	123	72
6.78 — 6.80	Swale	4	444	69	130	18
	Total	14	1025	71	302	49
Medium	Upper	3	33	48	17	76
	Lower	1	15	0	15	67
10.78 — 6.80	Swale	* NA	NA	NA	NA	NA
	Total	4	48	33	32	56
Medium	Upper	NA	NA	NA	NA	NA
	Lower	2	16	0	16	44
1.79 — 6.80	Swale	2	16	0	16	6
	Total	4	32	0	32	25
Low	Upper	9	14	21	11	18
	Lower	14	32	22	25	36
10.78 — 6.80	Swale	6	14	7	13	15
	Total	29	60	18	49	27

* NA = no measurement available

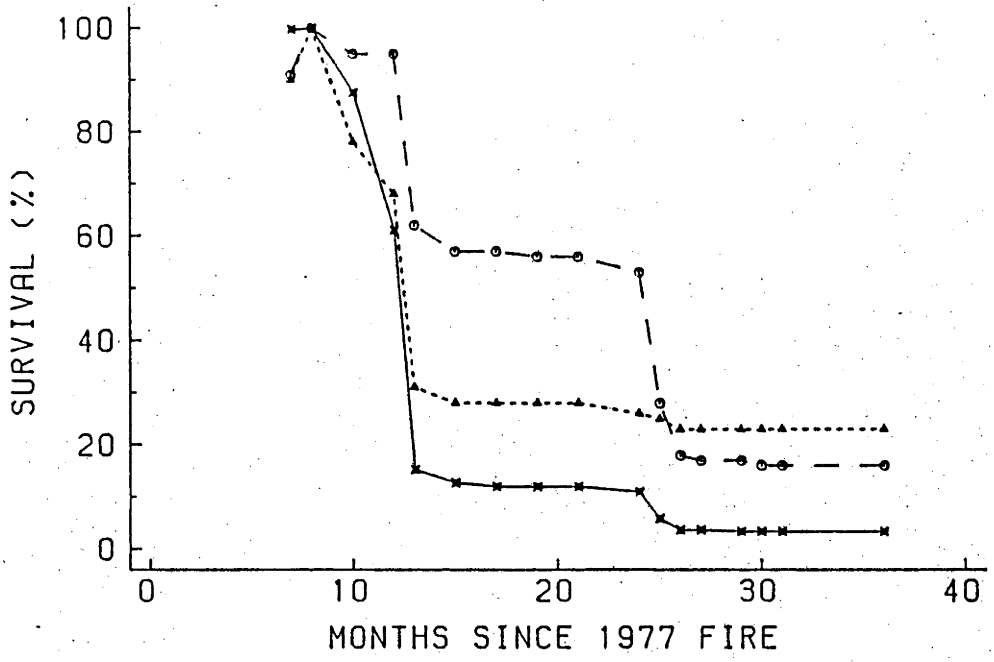


Figure 4.3a Survivorship of new genets in high density quadrats at three different topographic positions, viz:
Upper dune slope - solid line (n = 408 genets)
Lower dune slope - dashed line (n = 195)
Swale - dotted line (n = 422)

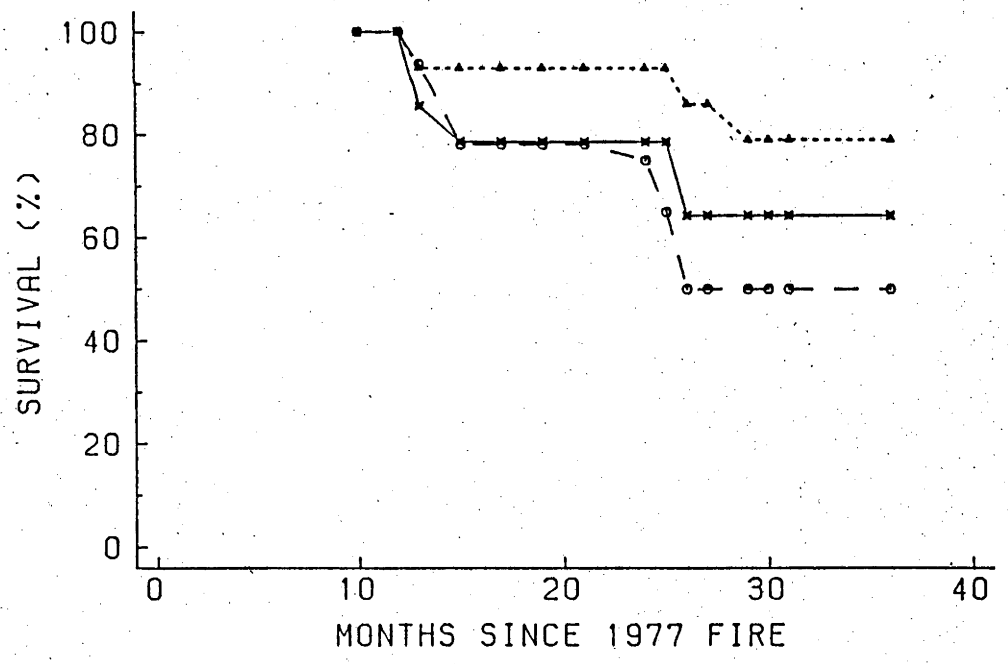


Figure 4.3b Survivorship of new genets in low density quadrats at three different topographic positions, viz:
Upper dune slope - solid line (n = 14 genets)
Lower dune slope - dashed line (n = 32)
Swale - dotted line (n = 14)

Despite some variation in mortality trends between the three different positions, it is evident that mortality was greatest on the dunes and least in the swales for both high and low density quadrats (Table 4.3, Figures 4.3a and 4.3b). However mortalities of seedlings and juveniles varied significantly between the different topographic locations for high density quadrats only (Table 4.4).

Table 4.4 Relationship between mortality and topography for seedlings and juveniles at two densities

Hypothesis tested		df	G	P
Mortality x topography independence:-				
(a) Seedlings :	High density	2	165.206	<.001***
	Low density	2	1.795	>.1
(b) Juveniles :	High density	2	88.544	<.001***
	Low density	2	2.432	>.1

The relationship between mortality and density was tested for both seedlings and juveniles growing at the three topographic positions (Table 4.5).

Density-dependent mortality was found to occur consistently on the upper dune slopes for both seedlings and juveniles, but varied in successive years in the lower slope and swale positions. Density-dependent mortality of seedlings occurred in the swales, but not on the lower slopes, whereas this result was reversed for juveniles.

Table 4.5 Relationship between mortality and density for seedlings and juveniles at three topographic positions.

Hypothesis tested		df	G	P
Mortality x density independence:				
(a) Seedlings:	Upper slopes	1	30.994	<.001***
	Lower slopes	1	2.927	>.05
	Swales	1	23.344	<.001***
(b) Juveniles:	Upper slope	1	10.819	<.01**
	Lower slopes	1	11.051	<.01**
	Swales	1	0.078	>.5

Genet mortality between 1978 and 1980 was largely confined to summer (Figure 4.2). Periods of summer drought associated with high temperatures occurred during this period (Section 3.2). Soil moisture in the upper 1m of the profile dropped to very low levels during the two summer periods (Section 3.6). It is therefore likely that limiting soil moisture was an important factor contributing to early mortality of genets. Detailed investigations of drought stress levels are described in Chapter 5.

A trend towards lower mortalities at less elevated topographic positions, as apparent in Figures 4.3a and 4.3b, implies that the factors contributing to mortality are generally not as severe in the swales. A comparison of initial mean seeding densitiies for high density quadrats on the upper slopes (68 genets m^{-2}) compared with the swales (111 genets m^{-2}) (Table 4.3) shows that the upper slope quadrats experienced higher mortality rates despite lower initial densities.

Variation in soil water relations as a result of differences in soil types and topographic factors probably contributed to this effect.

The change in the dependence of mortality on genet density in lower slope quadrats compared with swale quadrats over the two years (see Table 4.5) may have resulted from initial differences in genet densities (Table 4.3). If this is the case, then the higher mortality rates in lower slope quadrats in 1979/1980, despite similar juvenile densities, may reflect a greater severity of factors contributing to mortality on the lower slopes, compared to the swales. Differences in seasonal conditions between successive years may be important in this regard. It is also probable that mortality is influenced by the development of a lignotuber in juveniles and an enhancement of the ability to obtain soil moisture through greater root system development in older individuals.

4.4 Mortality of adults and coppicing lignotubers

4.4.1 Introduction

The fire at the study site in 1977 resulted in widespread stem death. Immediately following the fire, burnt adults were classified in terms of the mallee population model as 'stemless lignotubers' (Figure 2.1). By July 1978, the majority of lignotubers had begun coppicing, and therefore had entered the 'coppicing lignotuber' life stage. Lignotubers were monitored at the beginning and end of the two-year study period. Owing to the difficulty of determining whether lignotubers had commenced coppicing before death, the present section includes 'stemless lignotuber' mortalities in the 'coppicing lignotuber' mortality estimates.

4.4.2 Methods

A series of 10m wide transects were established to monitor mortality rates of adult mallees in recently-burnt and long-unburnt areas. Two transects were set up in September 1978, and another in October 1978, in the area burnt in 1977. The three transects totalled 2.0ha in area. A further three transects totalling 1.5ha in area were established in adjacent unburnt areas in October 1978. The unburnt areas selected were located as close as possible to the transect sites in the recently-burnt areas. All transects were oriented at right angles to the dunes to ensure that both dune and swale areas were sampled. The sites selected appeared superficially similar, although higher pre-burn genet densities occurred in the unburnt site.

Adults in the transect areas were tagged, mapped, identified to species, and the life stage to which they belonged was recorded (i.e. adult, dead adult, coppicing lignotuber, or stemless lignotuber). The transects were monitored in 1978 (in September and October), and again in August 1980, in order to provide estimates of the number of deaths over the period 1978 to 1980. Lignotubers which had not commenced coppicing by August 1980 were classified as dead.

4.4.3 Results and discussion

The percentage mortality of adults and coppicing (recently-burnt) lignotubers, measured over the period 1978 to 1980, are shown in Table 4.6. Mean genet densities in the recently-burnt area were considerably less than in the adjacent unburnt area, yet mortality rates in the recently-burnt area were significantly higher [$X^2_{(1)} = 30.562$***]. Mortality rates in many plant populations have been shown to be related to genet density, with denser stands exhibiting greater mortality rates

Table 4.6 Mortality of adults and coppicing lignotubers between October 1978 and August 1980.

	(Long-unburnt) Adults	(Recently-burnt) Lignotubers (coppicing)
Total area monitored (ha)	1.5	2.0
Total genets monitored	898	605
Mean genet density (genets ha^{-1})	599	302
Measurements 1978:		
# dead	16	7+
# non-coppicing	-	70
Measurements 1980:		
# dead	21	37++
Estimates 1978-1980:		
# which died	5	30
% mortality	0.6%	5.0%

Notes: + obviously long-dead prior to the 1977 fire.

++ still non-coppicing in 1980, presumed dead.

(Yoda et al. 1963). In this case however, the observed density differences would favour higher mortality rates in the unburnt stand. It is apparent therefore that the 1977 fire had an overriding effect on factors controlling mortality, causing an increase in the number of genet deaths in the burnt area in the two years following the fire.

It seems likely that fire plays a important role in opening up space in which new genets might establish in a mallee population. In the absence of fire, natural thinning rates of the adult mallees at the study sites are very low (Table 4.6), and it may require a very long period of thinning under these conditions before sufficient space is available for a major recruitment event to occur.

4.5 Causes of mortality in the early life stages

4.5.1 Introduction

Mortality rates during the early life stages (i.e. emergent seedlings, established seedlings, juveniles; see Figure 2.1) are much greater than those occurring during later stages of the life cycle (Sections 4.3 and 4.4). The processes controlling mortality in the early stages are therefore important in determining future population parameters (e.g. density, age structure). Moreover, these processes are likely to be amenable to investigation in a short-term study. The present section describes investigations into factors thought to be important in contributing to mortality of seedlings and juveniles.

The factors investigated included:

1. grazing effects due to large herbivores;
2. grazing effects due to insect herbivores;

3. effects of: (i) genet density,

(ii) soil moisture availability,

(iii) nutrient availability.

4.5.2 Grazing effects due to large herbivores

4.5.2.1 Methods

To determine the effects of grazing damage by large herbivores (e.g. rabbits, kangaroos, sheep) on early genet mortality, eight exclosures were erected close to sites where control quadrats had been established. The exclosures were sited to cover the range of topographic variation, and to include areas close to the edge as well as near the centre of the burnt area.

Each exclosure consisted of a 1.5m high wire-mesh fence (mesh size = 4.0cm), enclosing an area of 2 x 2m. The lower part of the fence was buried to 15cm to discourage burrowing. A $1m^2$ quadrat was located close to the centre of each exclosure and contained genets at a similar density to nearby control quadrats.

The exclosures were erected in December 1978, and surviving genets in each quadrat were monitored at the same time as the control quadrats (see Section 4.3).

On two occasions, kangaroo tracks were noticed inside an exclosure. However, despite slight trampling damage to two genets on one of these occasions, no other damage was noticed at any time. The general absence of tracks inside the exclosures, and other signs of entrance such as burrowing, indicated that the exclosures were effective.

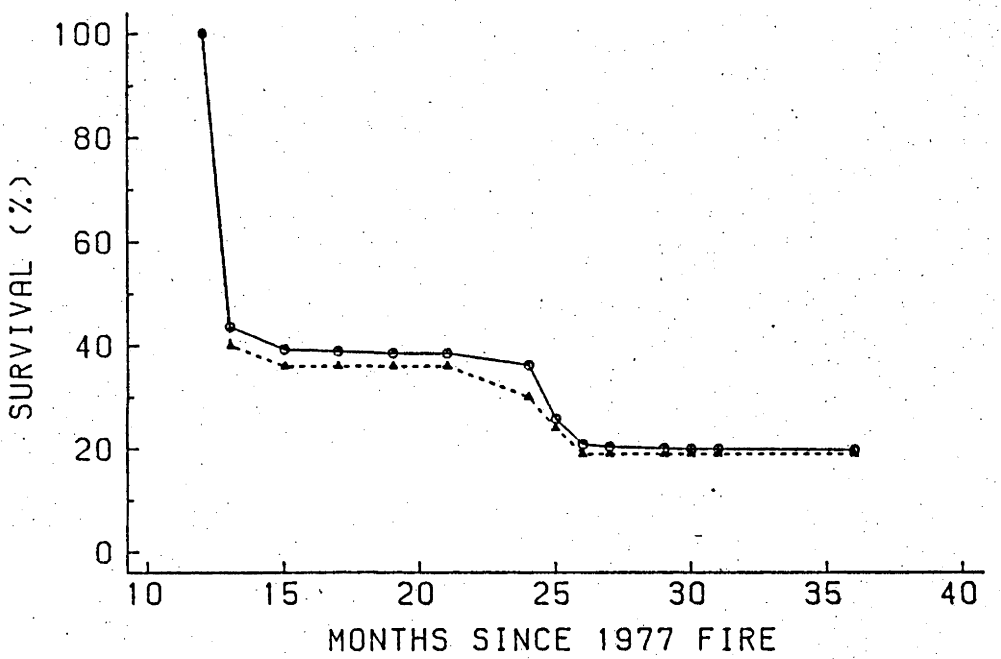


Figure 4.4 Survivorship of new genets protected from large herbivore grazing (dotted line) (n = 359 genets), compared with new genets in adjacent control areas (solid line) (n = 776). Survivorship is expressed as a percentage of genets present in December 1978. All genets were located in areas of high density.

4.5.2.2 Results and discussion

Casual observation indicated a general absence of grazing damage on new genets at the study site between 1978 and 1980. A comparison of mortalities of seedlings inside exclosures with nearby controls (see Table 4.7, Figure 4.4) demonstrated that the elimination of large herbivore grazing damage on young genets between December 1978 and August 1980, had no significant effect on mortality ($X^2_{(1)} = 0.127$, $P>0.5$). This does not preclude the possibility that grazing does occur. It is possible that heavy grazing by large herbivores is a localized phenomenon, or that it is widespread but of low incidence, and hence was not detected in the present experiment.

Table 4.7 The effects of large herbivore grazing on young genet mortality.

Treatment	Total number of genets (December 1978)	Genet density (m^{-2})	Number of survivors (August 1980)	Mortality %
Exclosures	359	44.9	68	81
Controls	776	55.4	154	80

4.5.3 Grazing effects due to insect herbivores

4.5.3.1 Methods

Preliminary estimates of the amount of leaf area lost on young genets due to insect grazing were made using line transects. The transects were oriented at randomly selected bearings, and were located

close to areas in which the monitored quadrats (Section 4.3) had been established. One hundred seedlings located along each transect were recorded. The leaf area loss due to insect damage was estimated for each of the leaves on the seedlings. Damage was scored using a ten point interval scale (viz:- 0 = <10% damage, 1 = 10-20%, 2 = 20-30%, etc.). Damage due to other causes (e.g. fungal lesions) was also noted. The mean percentage leaf damage due to insects was calculated for each seedling; these calculations were used to obtain a mean percentage leaf damage estimate for the sample population. Measurements were made using a single transect in May 1979, June 1979, July 1979, and September 1979.

To determine the effect of insect damage on early genet mortality, groups of juveniles were regularly sprayed with insecticides and their mortality rates compared with adjacent unsprayed groups. Three sites were selected: one close to the northern edge of the burn near an unburnt E. largiflorens stand; another in the centre of the burnt area; and a third close to an unburnt mallee stand at the western boundary of the burnt area. At each site, two parallel rectangular areas, separated by 3m, were marked out so as to include a minimum of fifty juveniles at similar densities. All sampling areas were situated at least 2m from the surrounding coppice.

One sampling area at each site was randomly selected and the juveniles within it were sprayed with a mixture of the two commercial insecticides: "Rogor" (Dimethoate 30% w/w), and "Buggeta" (D.D.T 12.5% w/w and Maldison 10% w/w) at the manufacturer's recommended dosage levels. This mixture was used since it includes both contact and systemic insecticides and is capable of affecting a wide range of insects. Spraying commenced in November 1979, was repeated at two-week intervals until late February 1980, and continued monthly thereafter.

Insect damage on both sprayed and unsprayed juveniles was estimated, as described above, at irregular intervals from November 1979 to June 1980.

4.5.3.2 Results and discussion

Initial estimates of leaf damage caused by insects are shown in Table 4.8.

Table 4.8 Estimates of seedling leaf damage due to insects during 1979.

Date	Location	Number of genets monitored	Mean % leaf damage
May 1979	Northern margins	200	7.4
June 1979	Central	200	5.3
July 1979	Central	100	11.6
September 1979	Northern margins	100	8.9

These estimates indicate that damage levels were generally low during 1979 (mean leaf damage = 8.3%). Considerable variability in the extent of leaf damage amongst seedlings was observed in many areas, with some individuals experiencing up to 50% leaf area loss. The majority of seedlings, however, exhibited much lower (ca 5%) leaf area loss. Damage to apices caused by sap-sucking bugs also occurred. Estimates of the extent of this type of damage were not obtained due to difficulties in locating the lesions.

Table 4.9 The effects of leaf area losses due to insects on seedling mortality.

Site	Treatment	Initial No. of genets[+]	Mean % leaf damage[++]	Total deaths[+++]	$X^2_{(1)}$ (mortalities)	P
Edge(near E. largiflorens)	Sprayed	63	4.8	21		
	Control	84	10.0	28	0	>.975
Centre	Sprayed	68	5.2	25		
	Control	87	8.6	33	.022	>.5
Edge(near unburnt mallee)	Sprayed	59	8.5	15		
	Control	54	12.0	11	.406	>.5
Pooled Results	Sprayed	190	6.2	61		
	Control	225	10.2	72	.001	>.9

Notes: + Number of genets in November 1979

++ Period Dec. 1979 to Mar. 1980

+++ Deaths to Mar. 1980

Comparisons between sprayed and control plants in terms of the effects of leaf area loss on juvenile mortality during the 1979/1980 summer are presented in Table 4.9. Despite the lower estimates of leaf area lost from the sprayed plants compared with the control plants at each site, there was no significant difference in mortality between the treatments, both when tested at each site, and over all sites (Table 4.9). It is apparent that leaf area loss due to insect damage was not a direct cause of juvenile mortality during the 1979/1980 summer. Recent evidence for subalpine Eucalyptus species indicates that insect grazing pressures severely depress plant growth and productivity (Morrow and La Marche 1978). It is possible that insects exert a similar effect on mallee eucalypts, and in this case, insect grazing may contribute to mortality indirectly by reducing growth and lowering plant vitality. Long-term monitoring would be required to investigate this effect.

4.5.4 Density, water, and nutrients

4.5.4.1 Methods

A three-factor experiment designed to investigate the effects of genet density, soil moisture availability, and nutrient availability on genet mortality, was set up in January 1979. A site located on a large, relatively flat (slope <3°) dune hummock, close to the southern margins of the burnt area, was chosen for the study. Within an area of 100 x 50m, twenty-five $1m^2$ quadrats were established in areas of high seedling density (>20 seedlings m^{-2}) and a further twenty-five in low density areas (<5 seedlings m^{-2}).

The high and low density quadrats were divided into five groups. Irrigation and fertilizer-addition treatments were each applied to a group of five high density and five low density quadrats. A further

five high density and five low density quadrats were maintained as controls. A double treatment (irrigation and fertilizer-addition) was applied to the remaining groups of ten high density and ten low density quadrats.

Irrigation involved the addition of 25 litres of water (the equivalent of 25mm depth of water) to each quadrat. Runoff was prevented with removable sheet-metal barriers. Uniform distribution of water over the quadrat area was ensured, and surface disturbance minimized, by using a hand-held sprinkler. Quadrats were irrigated monthly from February 1979 to November 1979, and fortnightly during the summer period December 1979 to February 1980.

The fertilization treatment involved the addition of two forms of fertilizer. A single slow release fertilizer pill ("Ritegro", Ryco Products Pty Ltd, Australia) was pushed into the ground at the base of each seedling in January 1979, and February 1980. A granulated, resin-coated, slow-release fertilizer ("Osmocote 14-6.1-11.6", Sierra Chemical Europe B.V., The Netherlands) was also added to the surface of the quadrats, at the manufacturer's recommended application rates for woody seedlings, during the period August 1979 to December 1980.

In order to minimize interactions between treatments, quadrats belonging to each treatment were clustered,and the control quadrats were located around the margins of the experimental area. The area was relatively uniform and it was regarded as unlikely that the separation of treatments would influence the results. Genet mortality was monitored at approximately two-monthly intervals between January 1979 and August 1980.

Percentage mortality data were transformed using the arcsine tranformation (Sokal and Rohlf 1969, p386), and the transformed data were tested for homoscedasticity and subjected to analyses of variance using the SPSS 'Anova' program (Nie et al. 1975). Equal cell sizes were obtained by randomly selecting five quadrats from the ten low density double-treatment quadrats. Five quadrats with the lowest initial genet densities were selected from the ten high density quadrats to ensure initially similar genet densities for the analysis of the high density treatments.

4.5.4.2 Results and discussion

The overall mortalities of genets in each of the treatments in the three factor experiment are presented in Table 4.10, Figures 4.5a and 4.5b. A three-way analysis of variance was conducted on transformed percentage mortality data for all quadrats (Table 4.11).

The analysis of variance indicated that density and fertilizer addition significantly influenced mortality, and that there was a significant interaction effect of density and irrigation on mortality (Table 4.11). However, the mortality data for the irrigation treatment (Table 4.10) demonstrated a higher percentage mortality in low density quadrats. This result, which contrasted with the trends for the controls and the fertilizer-addition treatment (Figure 4.5b), was caused by the death of three seedlings, compared to single deaths in the other low density treatments. To overcome a possible bias in the analysis resulting from comparing treatments between the two density classes with their widely differing genet totals, two-way analyses of variance were conducted separately on high and low density data (Table 4.12).

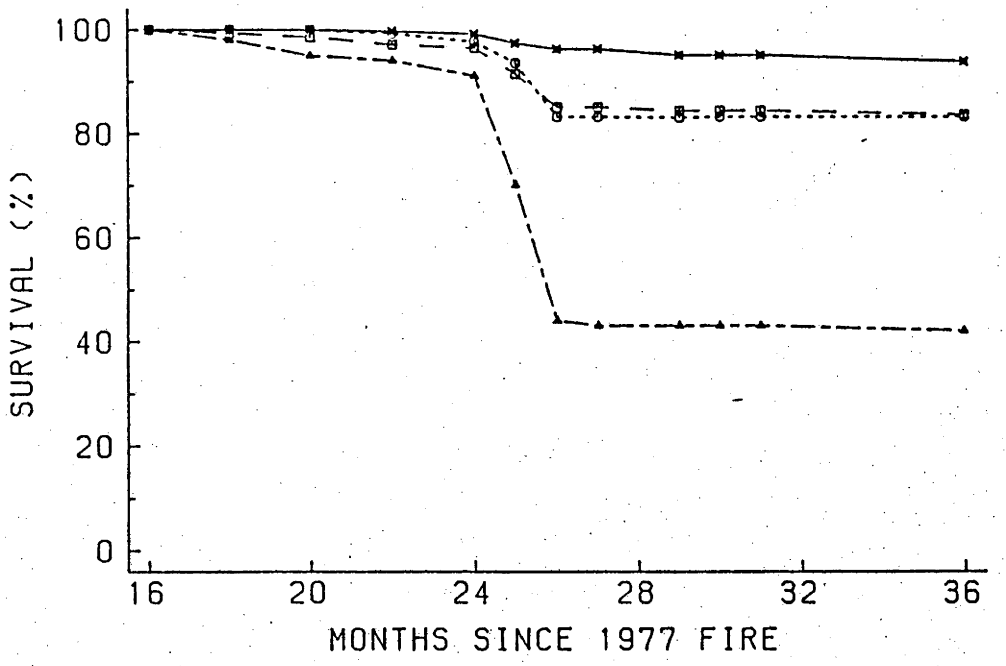


Figure 4.5a Survivorship of new genets in high density quadrats in response to:
Irrigation & Fertilization - solid line (n = 338)
Irrigation - dashed line, open symbols (n = 118)
Fertilization - dotted line (n = 124)
Controls - dashed line, closed symbols (n = 112)

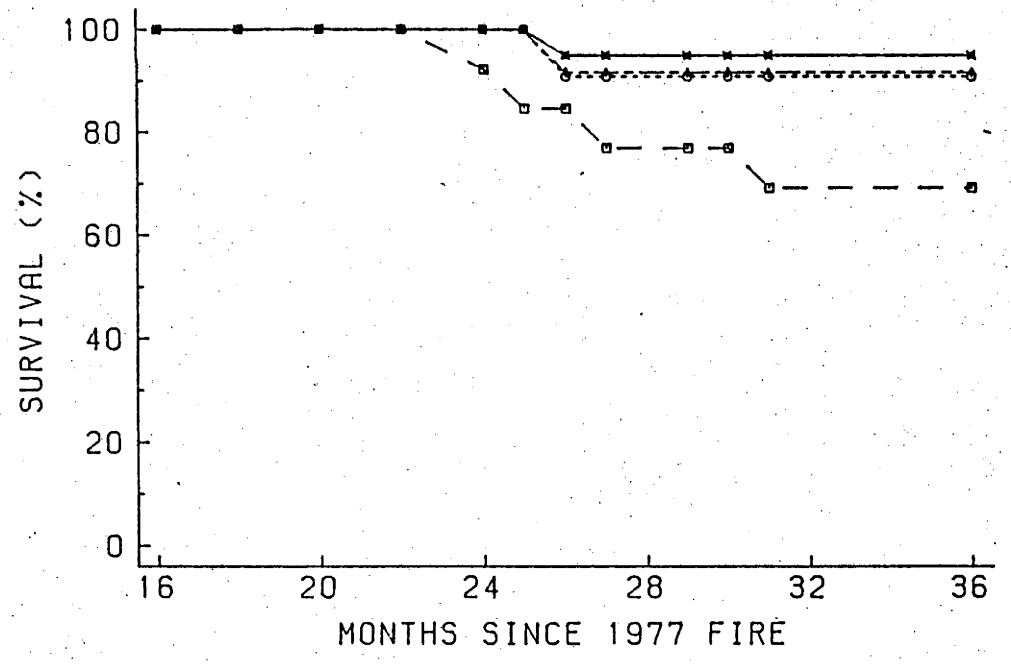


Figure 4.5b Survivorship of new genets in low density quadrats in response to:
Irrigation & Fertilization - solid line (n = 20)
Irrigation - dashed line, open symbols (n = 13)
Fertilization - dotted line (n = 11)
Controls - dashed line, closed symbols (n = 12)

Table 4.10 The effects of genet density, irrigation, and fertilizer-addition on mortality.

Treatment	Density	No. of quadrats	Total no. of genets	Total deaths to Mar 1980	% Mortality
Controls	High	5	112	64	57
	Low	5	12	1	8
Irrigated	High	5	140	21	15
	Low	5	13	3	23
Fertilized	High	5	124	21	17
	Low	5	11	1	9
Irrigated & Fertilized	High	5	338	14	4
	Low	5	20	1	5

Table 4.11 Three-way analysis of variance on transformed percentage mortality data for all quadrats (from Table 4.10)

Source of variation	df	F	P
Main effects:			
Density	1	11.929	.002**
Irrigation	1	2.448	.127
Fertilization	1	6.567	.015*
2-way interactions:			
Density x Irrigation	1	5.176	.030*
Density x Fertilization	1	1.528	.225
Irrigation x Fertilization	1	.103	.751
3-way interactions:			
Density x Irrigation x Fertilization	1	1.548	.222

Table 4.12 Two-way analyses of variance on transformed percentage mortality data for high and low density quadrats

Source of variation	df	F	P
High density quadrats:			
Main effects:			
Irrigation	1	15.600	.001**
Fertilization	1	15.268	.001**
2-way interactions:			
Irrigation x Fertilization	1	2.590	.127
Low density quadrats:			
Main effects:			
Irrigation	1	.165	.690
Fertilization	1	.576	.459
2-way interactions:			
Irrigation x Fertilization	1	.280	.604

The results of the two-way analyses of variance indicated that irrigation and fertilizer-addition treatments significantly influenced mortality of genets only in high density quadrats (Table 4.12). Neither increased soil moisture, nor increased nutrients had any significant effect on genet mortality at low densities. A possible explanation for this result is that genets in low density quadrats are less likely to experience resource limitations as a result of intraspecific competition. However, it is also possible that the number of genets

sampled in the low density quadrats was not large enough to provide a significant result. A calculation of the minimum sample size required to detect a significant difference between the low density irrigation treatment and the irrigation and fertilizer-addition treatment (see Sokal and Rohlf 1969, p 609), indicated that at least fifty-two genets in each treatment would be required to ensure an 80% probability of detecting a true difference between these two treatments at the 5% level of significance. Therefore no conclusions can be drawn from the results of the analyses of variance for low density treatments (Table 4.12). Practical limitations with the irrigation treatment precluded larger sample sizes.

Despite the problems with detecting significant differences amongst the results for low density treatments, it is apparent from a comparison of Table 4.10 with the results obtained in Section 4.3 that mortality rates are generally low amongst seedlings at low densities. It is likely, therefore, that resource limitations in low density situations are not as serious as in areas of high genet density.

The significant decrease in genet mortality in high density quadrats as a result of the irrigation treatment (Table 4.10) indicates that low soil moisture levels are an important factor contributing to genet mortality. This result supports the observations made in Section 4.3.

Reasons for the reduction in mortality caused by the fertilizer-addition treatment are not clear. It is possible that the higher nutrient levels during the year preceding the 1979/80 summer resulted in an increase in root development, thereby enhancing a fertilized plant's ability to obtain water from a larger soil volume, and perhaps more significantly from greater depths. However, this

hypothesis was not tested directly in the present study owing to practical difficulties associated with large-scale excavation work.

The irrigation and fertilizer-addition double treatment resulted in the lowest mortality rates for both high density and low density quadrats (Table 4.10). Although this result was not statistically different in low density treatments (see above), it was significantly different in the high density treatments (e.g. comparison of irrigated versus irrigated and fertilized: $X^2_{(1)} = 17.199$, $P<.001$***). Since no significant interactions between irrigation and fertilizer addition were detected by the analyses of variance (Tables 4.11 and 4.12), it was concluded that the effects of these treatments were additive.

4.6 Summary and general discussion

The fire which occurred near Lake Albacutya in December 1977 resulted in a significant recruitment event. Estimates of numbers of newly-germinated seedlings present in September 1978 indicate minimum recruitment rates of ca 10^4 ha^{-1}. Post-fire genet densities were considerably higher than pre-fire genet densities (ca 3×10^2 ha^{-1}).

Mortality rates of new genets in the two years following the fire were high (ca 75%). Mortality was greatest at more elevated positions on the dunes, and least in the swales, for seedlings at similar densities. Density-dependent mortality was consistently high at upper slope positions, but varied in significance between successive years for lower dune slopes and swale locations. Mortality of new genets was largely confined to the summer months when prolonged, dry periods with high temperatures occurred.

Investigations of possible causes of mortality of new genets indicated that grazing effects due to both large herbivores and insects did not significantly influence mortality. A three-factor experiment investigating the effects of genet density, soil moisture availability and nutrient availability confirmed the previous observation that high genet densities result in significantly higher mortality rates. Increases in either soil moisture, or nutrient levels significantly reduced mortality rates in areas of high density. The combination of these factors caused an even greater reduction in mortality. Similar trends were noted in replicates with low seedling densities, but insufficient data was available to determine whether these trends were significant.

Mortality rates of long-unburnt adults over the two year study period were low (ca 0.6%). A comparison of mortality rates between young genets and adult genets indicated that general mortality trends throughout the life-cycle conform to the Type III survivorship distribution with initial very high mortalities but low mortalities for the greater part of the life-cycle (see Section 4.1).

Fire in an adult population causes widespread stem death. Estimates of mortality amongst recently-burnt, coppicing lignotubers indicated an increase in genet mortality rates (5.0% in two years) compared with the rates for an adjacent unburnt stand. Fire therefore appeared to cause an increase in adult/coppicing lignotuber mortality rates. This effect may be important in hastening the thinning process, and releasing space in which new genets can establish. If most fires cause a similar increase in mortality rates amongst recently-burnt genets, then it is likely that the long, flat tail of the Type III survivorship curve is punctuated by a series of small drops corresponding to the fire regime.

At the end of the two year study period, a substantial number of newly-recruited genets remained alive (ca 2.5×10^3 seedlings ha^{-1}). These had entered the juvenile life stage and presumably had acquired some resilience to adverse environmental conditions through the enhanced regenerative potential imparted by the development of a lignotuber. It is likely that, with the exception of continued high thinning rates in high density areas, the mortality rates of these juveniles would become less over the next few years. In this case, it is possible that a number of new genets might survive to become part of the adult population.

Most mallee populations probably have a complex age structure. Successful recruitment of new genets into the population from infrequent germination events is likely to be contingent on post-fire mortality rates of coppicing lignotubers, which in turn might be dependent on the age structure of the population. However, climatic conditions in the years following the fire are also crucial: the combination of these factors may impart a highly stochastic nature to recruitment and therefore to population age structure.

CHAPTER FIVE

DROUGHT STRESS

CHAPTER 5

DROUGHT STRESS

5.1 Introduction

High mortality rates were observed amongst new genets of E. incrassata at the study sites during the period 1978 to 1980. Investigations described in the previous chapter demonstrated that mortality was confined to summer when long, dry periods occurred, and soil moisture dropped to very low levels. An irrigation treatment was found to significantly decrease mortality (Section 4.5.4). It therefore seemed likely that drought stress induced by soil moisture limitations was an important factor contributing to genet mortality.

Many plants characteristic of drought-prone environments have evolved strategies for avoiding drought injury: these strategies include both 'drought-avoidance' and 'drought-tolerance' (Levitt 1972). Drought avoidance may be achieved through conservation of water, resulting in the maintenance of high internal water potentials despite decreasing environmental water potentials. Drought tolerant plants avoid dehydration at low internal water potentials by reducing their osmotic potential below that of their environment, or alternatively are able to tolerate dehydration through metabolic readjustment or structural modifications (Levitt 1972).

Eucalypts appear primarily to be drought avoiders (Foster 1979). There is also evidence that drought-hardened populations of some eucalypt species are able to tolerate low internal water potentials by an increase in resistance of their protoplasm to desiccation (Ladiges

1974) and as a result of structural changes associated with an increase in sclerophylly (Collatz et al. 1976).

Seedlings of E. incrassata which survived the first summer (1978/79) were probably either growing in situations which afforded some protection from drought stress, or alternatively possessed some mechanism for avoiding or tolerating high stress levels. The second summer (1979/80) was exceptionally dry, with only 6.4mm of rain recorded between 26 November 1979 and 8 March 1980. Local weather conditions during February included twelve days with temperatures above 36°C and relative humidity below 20%. This chapter describes investigations of drought stress in juveniles of E. incrassata, conducted during February 1980 and March 1980. The aims of these investigations were to determine:

1. leaf water potentials in juveniles showing visible signs of drought stress (i.e. leaf discoloration);
2. whether highly-stressed juveniles could recover when irrigated;
3. whether the irrigation treatments described in Section 4.5.4 affected either the degree to which juveniles were stressed in February 1980 or the extent of recovery following further irrigation in February 1980;
4. whether large juveniles experienced different levels of stress from small juveniles;
5. whether juveniles growing on the upper parts of dunes were subjected to greater stress than juveniles growing in swales;
6. stress levels in coppicing adults;
7. the effects of different stress levels on leaf conductance and transpiration;

5.2 Measurement of leaf water potential(Ψ)

5.2.1 Introduction

There are several parameters which may be used for assessing plant water status. These include: water potential, relative water content, tissue water content, and fresh weight (Hsaio 1973). Of these parameters, leaf water potential has become widely accepted as a useful and sensitive indicator of plant water status (Lange 1975). A standard technique for measuring leaf water potentials in the field involves the use of a pressure chamber (Scholander et al.1965); this technique was used in the present study.

5.2.2 General methods

The water potentials of fully-expanded leaves were determined using a pressure chamber similar to that described by Scholander et al.(1965). The technique used closely followed that recommended by Ritchie and Hinckley (1975). Individual leaves were cut from selected juveniles. To ensure minimal water loss, water potential determinations were always made within one minute of detaching the leaf from the plant. Water potential determinations made on different leaves from the same juveniles were highly consistent. Seedlings were generally small (< 50 leaves), and thus to minimize the effect of removing leaves, subsequent estimates were made only on a single leaf per juvenile on each day of measurement. Occasional replications were made to further check the consistency of measurements.

Measurements were made before dawn, when leaf water potentials were at their highest levels. In certain instances, additional measurements were made between 12.00 hours and 14.00 hours, and on one occasion (2

April 1980), a diurnal course of hourly measurements was made. Except where otherwise mentioned, water potential values refer to predawn measurements.

Initial water potential determinations were made during the period 14 to 27 February 1980, and follow-up measurements were made in March, April and June 1980, spanning a total period of 120 days. - Most juveniles investigated were located in the vicinity of the large, flat dune hummock used for the irrigation/fertilization experiment (Section 4.5.4). The comparative measurements between juveniles growing on dune crests and in swales were made at two sites approximately 1.5 km south of this site.

The t-test for the heteroscedastic case (Sokal and Rohlf 1969, p 374) was used for comparisons of water potential levels between groups of juveniles. It was regarded as likely that any deviations from normality in the water potential data would result in the distributions of the magnitude of water potential being left-skewed due to juvenile mortality at high stress levels. This type of deviation would result in a conservative bias in an analysis of the differences between the means of stressed and unstressed sample groups. Because of the small sample sizes, heteroscedasticity was assumed so as to further ensure a conservative analysis. Where estimates of sample variability are shown, the standard deviation is included with the mean unless otherwise stated.

5.2.3 Visibly-stressed juveniles

5.2.3.1 Methods

Ten juveniles exhibiting signs of stress (viz: a yellowish leaf colour and death of the lower leaves) were selected and measurement of their leaf water potentials commenced on 15 February 1980. Five of these juveniles were irrigated the day after measurements commenced by adding 20 litres of water to an area of about 1 m^2 surrounding each juvenile. A further two juveniles were irrigated in a similar fashion three days later. Plants were irrigated only once. Predawn leaf water potentials were monitored either at one or two day intervals between 15 and 27 February 1980, and subsequently at irregular intervals until June 1980.

Another group of ten visibly-stressed juveniles was selected on 23 March 1980. Predawn water potential measurements were made on each of the juveniles at two-day intervals between 23 March 1980 and 2 April 1980 and at irregular intervals until June 1980. This group of ten juveniles was also used for measurements of stomatal conductance (see Section 5.3.4).

5.2.3.2 Results and discussion

Short-term and long-term changes in predawn leaf water potential for both irrigated and non-irrigated (control) juveniles selected in February 1980 are shown in Figures 5.1 and 5.2 respectively. Figure 5.2 also shows daily rainfall totals for Rainbow P.O. between 14 February 1980 and 15 June 1980.

In February 1980, juveniles with visible signs of stress exhibited low predawn water potentials (Mean Ψ = -5.3 $\pm$ 0.7 MPa). Measurements of the photosynthetic characteristics of seedlings of the mallee

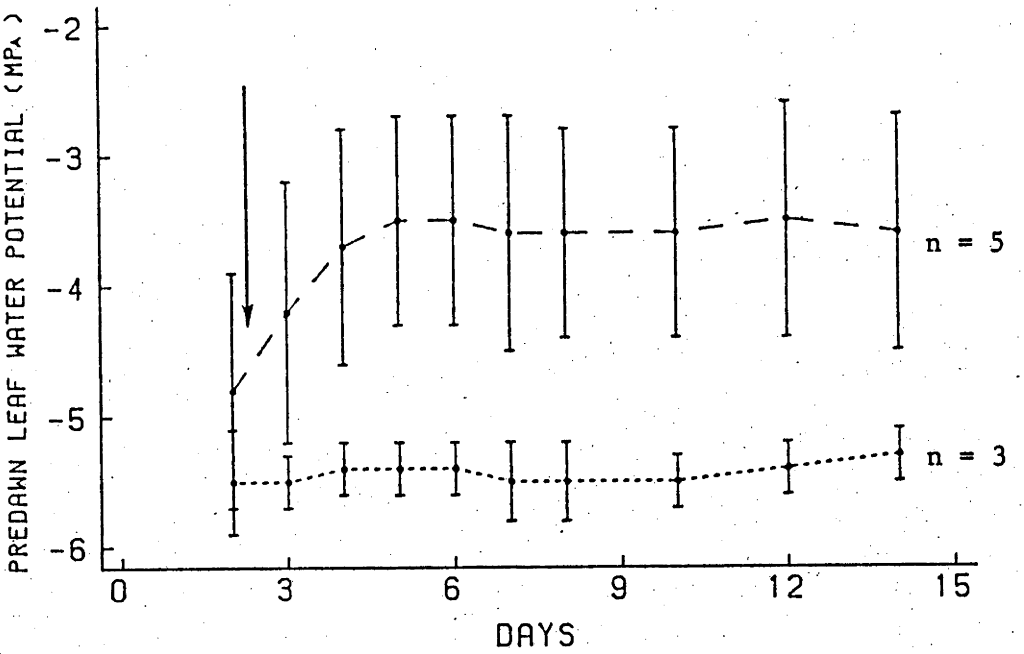


Figure 5.1 Short-term changes in predawn leaf water potential for irrigated (dashed line), and non-irrigated (dotted line) juveniles. Arrow indicates irrigation. Bars represent 95% confidence intervals. (February 1980)

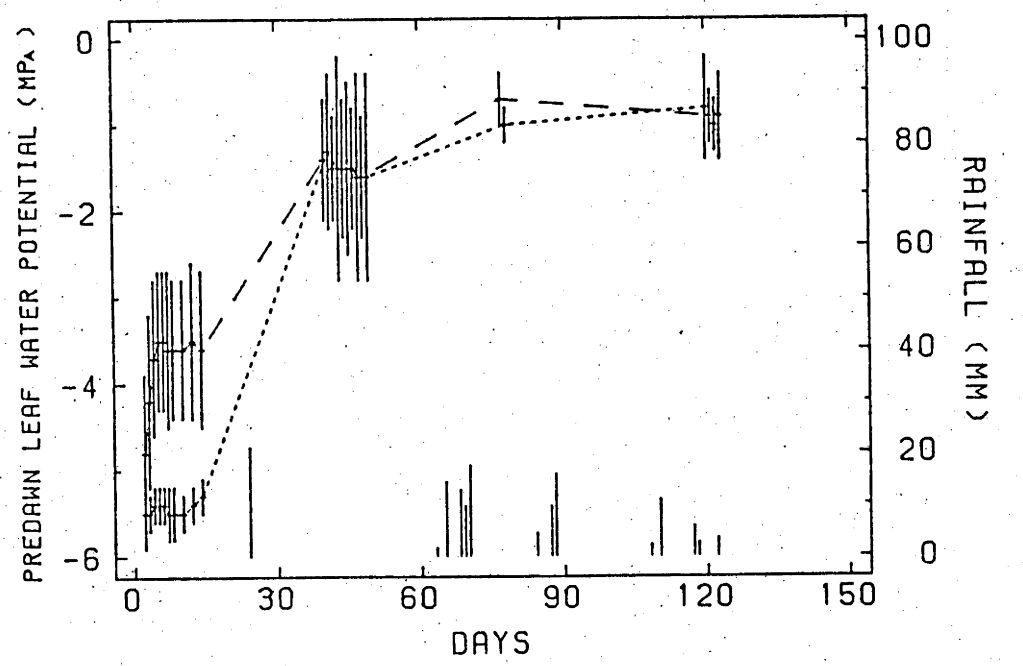


Figure 5.2 Long-term changes in predawn leaf water potential for the irrigated and non-irrigated juveniles shown in Figure 5.1. Daily rainfall totals for Rainbow P.O. between 14 February and 15 June, 1980 are also shown.

E. socialis gradually exposed to drought stress under laboratory conditions indicated that a marked reduction in carbon assimilation occurred at leaf water potentials below -1.5 MPa, and that rates of assimilation approached zero below -3.0 MPa (Collatz *et al.* 1976). It is therefore likely that the visibly-stressed *E. incrassata* juveniles monitored in February 1980 were also experiencing low rates of carbon assimilation as a result of the dry conditions.

Irrigation of visibly-stressed juveniles in February 1980 resulted in significant increases in predawn leaf water potentials during the fourteen day monitoring period following irrigation (Figures 5.1 and 5.2). Recovery did not appear to be related to the pre-irrigation levels of predawn leaf water potential.

The drought ended with substantial rainfall on 8 March 1980 (20.8mm, Rainbow P.O.). This single rainfall event caused a significant recovery from the low February 1980 predawn leaf water potentials (Figure 5.2 and Table 5.1). There was no longer any significant difference in stress levels between the irrigated and non-irrigated juveniles when further measurements were made in late March 1980 (Figure 5.2). Additional rainfall up to June 1980 caused little further change in levels of predawn leaf water potential.

The group of ten visibly-stressed juveniles selected on 23 March 1980 showed a range of predawn leaf water potentials between -2.0 MPa and -4.0 MPa. Measurements had not been made on these juveniles in February 1980, but from a consideration of the trends in Figure 5.2, it seems likely that they would have been under greater stress than when monitored in March 1980 after the rain.

A comparison was made between the levels of predawn leaf water potential of the two groups of visibly-stressed juveniles monitored in February 1980 and March 1980 respectively (Table 5.1).

Table 5.1 Comparison of predawn leaf water potentials for two different groups of visibly-stressed juveniles monitored in February 1980 and March 1980

Comparison	Mean Ψ (MPa)	df	t	P
February 1980 vs	-5.3			
March 1980	-3.0	9	7.107	<.001***

The comparison indicated a significant difference in predawn leaf water potentials between these two groups of juveniles. It should be noted however, that this represents an unmatched comparison, and it is possible that inherent differences between the two groups may also have influenced the result.

The results presented in this section demonstrate that E. incrassata juveniles experience high levels of drought stress as a result of long dry summer periods. A single irrigation, or a single rainfall event of ca 20mm can result in a significant reduction in stress.

5.2.4 Apparently-healthy juveniles

5.2.4.1 Methods

Despite the exceptionally dry conditions preceding February 1980, many juveniles retained a healthy appearance. Predawn leaf water potential deteminations were made on a group of ten apparently-healthy juveniles on 15 February 1980. A comparison was made between this group and the ten visibly-stressed juveniles monitored in February 1980.

Ten juveniles which had been irrigated during the previous twelve months in parallel with the irrigation experiment described in Section 4.5.4 were also monitored in February 1980. The predawn leaf water potentials of these juveniles were compared with the ten apparently-healthy juveniles referred to above.

Also in February 1980, a group of sixteen juveniles showing no obvious signs of stress were selected such that there were four individuals in each of the following categories: large (>30 leaves) and previously irrigated; small (<15 leaves) and previously irrigated; large and not previously irrigated; small and not previously irrigated. 'Previously irrigated' juveniles had been irrigated in parallel with the three factor experiment described in Section 4.5.4. Measurements of predawn leaf water potentials commenced on 14 February 1980. Two juveniles in each category were subsequently irrigated on 15 February 1980 with 20 litres of water. Predawn leaf water potentials were monitored until June 1980.

In March 1980, at the same time as the second group of ten visibly-stressed juveniles was selected (Section 5.2.3.1), a further group of ten apparently-healthy juveniles was also chosen such that each of the apparently-healthy juveniles was growing in close proximity to an

apparently-stressed juvenile. These matched pairs were used for stomatal conductance measurements (see Section 5.3.4). A comparison of levels of predawn water potential was also made between these two groups.

5.2.4.2 Results and discussion

Results of the comparisons between apparently-healthy and visibly-stressed juveniles, and apparently-healthy and previously-irrigated, apparently-healthy juveniles are shown in Table 5.2.

Table 5.2 Comparisons of predawn leaf water potential for apparently-healthy juveniles with visibly-stressed and previously-irrigated juveniles (February 1980)

Comparison	Mean Ψ (MPa)	df	t	P
Healthy vs	-3.7			
Visibly-stressed	-5.3	9	4.177	<.01**
Healthy vs	-3.7			
Previously-irrigated	-2.8	9	2.758	<.05*

These results indicate that in February 1980, juveniles without visible signs of stress had significantly higher predawn leaf water potentials than juveniles that were visibly-stressed. Although conditions prior to monitoring had been very dry, there appears to have been a considerable range in levels of internal water potential.

It is also evident from Table 5.2 that the long-term irrigation treatment had resulted in significant reductions in February 1980 stress levels compared to non-irrigated, apparently-healthy plants. Low mortality rates were observed in irrigated quadrats (Section 4.5.2). It would appear therefore that the high mortalities observed for non-irrigated juveniles were associated with water stress. The high predawn water potentials observed for the previously-irrigated plants probably resulted from December 1979 and January 1980 irrigations.

A comparison was made between the 27 February 1980 levels of predawn water potential of the seven visibly-stressed juveniles irrigated on 15 February 1980 (Section 5.2.3) and the ten apparently-healthy juveniles (Table 5.3).

Table 5.3 Comparison of predawn leaf water potentials for apparently-healthy and visibly-stressed, irrigated juveniles two weeks after the irrigation (27 February 1980)

Comparison	Mean Ψ (MPa)	df	t	P
Stressed, irrigated vs	-3.5	6		
Healthy	-3.8	9	0.574	>.5

This comparison indicated that the addition of 20 litres of water to visibly-stressed juveniles had increased their predawn water potentials to a level similar to that of the apparently-healthy juveniles. E. socialis seedlings with water potentials below -3.0 MPa were shown to be drought-stressed (Collatz et al. 1976). Measurements of stomatal conductance made on E. incrassata juveniles in March 1980

(see Section 5.3.4) indicated that predawn water potentials below -3.0 MPa caused significant reductions in leaf conductance, and a likely reduction in photosynthesis. It appears, therefore, that although the irrigation of each visibly-stressed juvenile with 20 litres of water caused a significant increase in February 1980 predawn leaf water potentials, the amount of water used was insufficient to alleviate drought effects. The apparently-healthy juveniles may also have been suffering drought effects such as reduced assimilation in February 1980, but plant water potentials had not yet reached sufficiently low levels for visible tissue damage to occur.

The visibly-stressed plants selected in March 1980 had significantly lower predawn leaf water potentials than adjacent apparently-healthy plants (also selected in March 1980) (Table 5.4).

Table 5.4 Comparison of predawn leaf water potentials for apparently-healthy and visibly-stressed juveniles selected in March 1980

Comparison	Mean Ψ (MPa)	df	t	P
Healthy vs	-1.4			
Visibly-stressed	-3.0	9	5.643	<.001***

It was apparent that, despite the 20.8mm of rain which fell on 8 March 1980 and significantly reduced stress levels (Figure 5.2), some juveniles were still experiencing low water potentials.

A non-matched comparison was made between predawn leaf water potentials of the two groups of apparently-healthy plants selected in February 1980 and March 1980 respectively (Table 5.5).

Table 5.5 Comparison of predawn leaf water potentials between two groups of apparently-healthy juveniles monitored in February and March 1980 respectively

Comparison	Mean Ψ (MPa)	df	t	P
February vs	-3.7			
March	-1.4	9	6.811	<.001***

This result supports the observations made for visibly-stressed juveniles (Figure 5.2), viz: rainfall in March 1980 resulted in a significant increase in predawn leaf water potentials. However, since the comparison was a non-matched one, it is possible that other factors (e.g. differences in drought tolerance) could have influenced the result.

Short term changes in predawn leaf water potentials following irrigation of juveniles in each of the four categories described in Section 5.2.4.1 are shown in Figure 5.3. Comparisons of the maximum changes which occurred in predawn leaf water potentials during the fourteen day monitoring period in February 1980 were made for each treatment using one-way analyses of variance on pooled data. Both the direction and magnitude of change were considered in each analysis (Table 5.6).

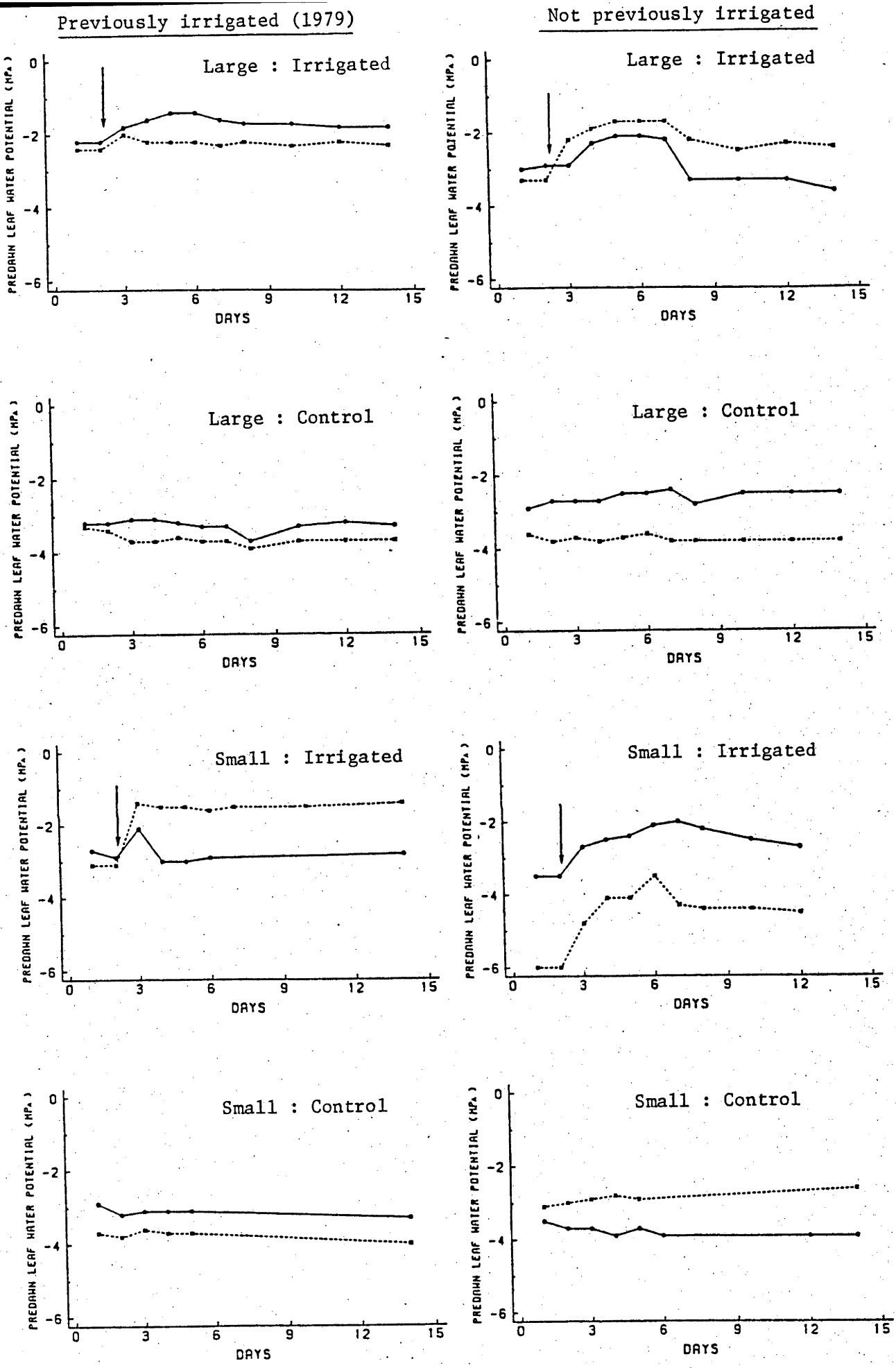


Figure 5.3 Changes in predawn leaf water potential of large and small juveniles as a result of two irrigation treatments. Arrows indicate 1980 irrigation. Dotted and solid lines represent separate juveniles.

Table 5.6 One-way analyses of variance on changes in predawn water potential during February 1980 as a result of the treatments described in Section 5.4.2.1

Source of variation	df	F	P
Size:			
between groups	1	.761	.398
Long-term irrigation:			
between groups	1	1.387	.259
February 1980 irrigation:			
between groups	1	24.584	.002**

The irrigation treatment on 15 February 1980 resulted in a significant increase in predawn leaf water potential (Table 5.6), whereas non-irrigated (control) juveniles maintained relatively constant levels of predawn water potential. Recovery appeared to be temporary in most cases since predawn leaf water potentials had commenced to fall again before monitoring ceased (Figure 5.3). The long-term irrigation had no significant effect on maximum change in water potential. However a visual comparison of the changes in predawn leaf water potentials indicates that plants which had been previously irrigated experienced smaller changes in predawn water potential following the February 1980 irrigation than plants which had never been previously irrigated. The reasons for this difference are not clear. It is possible that the long-term irrigation treatment had resulted in irrigated plants having

smaller root systems and therefore a reduced capacity to take up water rapidly in comparison to drought-hardened juveniles. Plant (shoot) size did not appear to influence the maximum change in predawn water potentials as a result of the February 1980 irrigation (Table 5.6).

It should be noted that these comparisons are based on pooled data and small sample sizes (n=8), and therefore the results must be viewed with some caution. The significance of the effect of the February 1980 irrigation in increasing plant water potentials is supported by previous results (Section 5.2.3). Changes in predawn leaf water potential of small juveniles in the above categories were not monitored after February 1980 owing to the limited number of leaves on these juveniles. Long-term changes in predawn leaf water potential for the large juveniles in all categories were similar to those shown in Figure 5.2.

The results presented in this section indicate that in February 1980, apparently-healthy juveniles had significantly higher predawn leaf water potentials than visibly-stressed juveniles. However, evidence from another study (Collatz et al. 1976) indicated that plants with water potentials below -3.0 MPa may be suffering drought stress. A previous long-term irrigation treatment up to January 1980 resulted in a significant reduction in stress levels experienced during February 1980. The irrigation of visibly-stressed juveniles with 20 litres of water in February 1980 resulted in an increase in predawn water potentials to a level similar to that of surrounding, non-irrigated, apparently-healthy juveniles.

Juveniles which were visibly stressed in March 1980 had significantly lower predawn leaf water potentials than adjacent apparently-healthy plants. Rainfall on 8 March 1980 resulted in a significant increase in water potentials of apparently-healthy plants.

5.2.5 Juveniles on crests and in swales

5.2.5.1 Methods

Predawn leaf water potentials of twenty-four large (>30 leaves) and twenty-four small (<15 leaves) juveniles were measured between 22 February and 28 February 1980. Twelve of each size class were located on dune crests, and the remainder in the adjacent swales. Only plants with no visible signs of stress were selected.

5.2.5.2 Results and discussion

The results of comparisons of predawn leaf water potentials between groups of large and small juveniles growing on crests and in swales are shown in Table 5.7.

Table 5.7 Comparisons of predawn leaf water potentials between large and small juveniles growing on crests and in swales in February 1980 (df=11) (sample means are shown)

	Crest	Swale	(t-test) t	P
Large	-4.6 MPa	-2.7 MPa	8.019	<.001***
Small	-3.8 MPa	-3.5 MPa	1.341	>.2
(t-test) t	2.507	-4.200		
P	<.05*	<.01**		

Small juveniles had similar leaf water deficits irrespective of whether they were located on a dune crest, or in a swale (Table 5.7). Large juveniles located on crests exhibited significantly greater levels of water stress than all other other juveniles; large juveniles growing in swales were least stressed.

The results presented in Section 4.3 showed that greater genet mortality occurs at more elevated positions on the dunes, and led to the hypothesis that limiting soil moisture on the dunes might result in higher levels of drought stress than in the swales. Although gravimetric determinations of soil moisture content indicated a higher water content in swale soils than dune soils, this does not always indicate a higher water availability (see Section 3.6). However the levels of predawn leaf water potential measured in large juveniles on crests and in swales in February 1980 indicate that swale soils probably have a greater water availability as well as a higher water content compared to dune soils. Water stress is therefore likely to be an important factor contributing to the greater observed mortality on crests, at least for large individuals.

The reasons why small juveniles experienced similar levels of predawn leaf water potential both on crests and in swales are not clear. It is possible that factors such as increased competition for soil moisture from other species may be important in the swales, effectively reducing available soil moisture levels near the surface; this might affect small juveniles more than large ones with deeper, more extensive root systems. Observations indicate that considerably more herbaceous vegetation occurs in swales than on the dunes.

Factors such as root/shoot ratios may have an important bearing on the observed variation in predawn water potentials in large and small plants depending on topographic location. Large juveniles (>30 leaves) possess considerably more evaporative surface area than small juveniles (<15 leaves). The water potential comparisons imply that the amount of evaporative surface area is likely to be a critical factor influencing survival on dunes during a summer drought. A large amount of leaf area, which is likely to be advantageous in providing assimilate for growth during other times of the year, may be disadvantageous during long, dry periods. Even if large juveniles possess larger root systems, these would only be of advantage whilst soil moisture levels remained high. Once soil moisture fell below a critical level, a large root system would no longer be able to offset water losses from a large evaporative surface area.

In the swales however, it is an advantage to be large (Table 5.7). Soil moisture is apparently adequate at swale sites, even during long, dry periods, since large juveniles at these sites were not suffering high levels of water stress in February 1980. A combination of higher soil moisture levels, together with more-developed root systems may provide large juveniles with the means to overcome water losses due to evaporation from their greater leaf area, and so obtain a competitive advantage over smaller juveniles in swales. The similar stress levels experienced by small juveniles at the two sites may therefore result both from a lower rate of water loss from small juveniles on dune crests, and an inability to take full advantage of the higher soil moisture content in swale soils due to poor root system development, and to competition from the denser surrounding vegetation.

5.2.6 Coppicing lignotubers

5.2.6.1 Methods

Measurements of predawn water potential were made on leaves from coppicing lignotubers growing in the vicinity of the juveniles described in Sections 5.2.3 and 5.2.4. Five lignotubers were selected on 14 February 1980 and a further five were selected on 23 March 1980. Predawn leaf water potential determinations were made at irregular intervals until June 1980.

5.2.6.2 Results and discussion

The levels of predawn leaf water potential measured for coppicing lignotubers in February 1980 were significantly higher than those measured in surrounding juveniles (Table 5.8).

However, a comparison of coppicing lignotubers and apparently-healthy juveniles selected in March 1980 indicated no significant difference in predawn leaf water potentials (Table 5.8). February 1980 measurements of predawn water potentials were similar to March 1980 measurements made on the same coppicing lignotubers, despite the early March rainfall. It appears that coppicing lignotubers were not suffering water stress in February 1980, and that the early March rains, which caused a significant increase in water potential in juveniles (Figure 5.2), had no significant effect on the coppicing lignotubers. It is likely that established lignotubers have root systems capable of tapping deep soil moisture supplies, thereby enabling them to avoid low water potentials even during prolonged summer droughts. Newly-established juveniles are apparently unable to tap the same water resources, and therefore are more prone to drought stress.

Table 5.8 Comparisons of predawn leaf water potentials for groups of coppicing lignotubers and apparently-healthy juveniles selected in either February 1980 or March 1980 and for a group of coppicing lignotubers monitored in February and March 1980

Comparison	Mean Ψ (MPa)	df	t	P
Coppicing lignotubers vs	-2.4	4		
Healthy juveniles (Feb 1980)	-3.7	9	4.296	<.01**
Coppicing lignotubers vs	-2.1	4		
Healthy juveniles (Mar 1980)	-1.4	9	1.565	>.1
Coppicing lignotubers:				
Feb 1980 vs	-2.4	4		
Mar 1980	-1.8	4	2.544	>.05

One coppicing lignotuber from the five selected in March 1980 exhibited predawn leaf water potentials below -3.7 MPa during March 1980, and did show some leaf discoloration. All other lignotubers examined were able to maintain predawn water potentials above -2.5 MPa. By June 1980, levels of predawn leaf water potential in all ten lignotubers were above -1.5 MPa.

The development of water stress in coppicing lignotubers may be a factor in contributing to the increased mortality rates observed in the recently-burnt site (Section 4.4). Water stress may also be important in contributing to adult mortality in times of extreme drought.

5.3 Measurement of stomatal conductance

5.3.1 Introduction

Stomatal regulation of water loss is a common drought-avoidance strategy among plants (Levitt 1972). Stomatal closure associated with increasing water stress usually results in a reduction in transpiration and a concomitant slowing of the decline of internal water potential. Low water status of photosynthetic tissues may also result in a reduction in, and eventually a cessation of, carbon assimilation (Cowan 1981). Plants which have ceased to assimilate carbon because of a low internal water status are regarded as stressed.

In association with the water potential determinations described in the previous section, estimations of stomatal conductance and transpiration rates were used to further assess the development of water stress in E. incrassata juveniles.

5.3.2 General methods

Measurements of stomatal conductance were made using a 'Delta-T Mk II' diffusion porometer (Delta-T Devices, Cambridge, England; see Stiles et al. 1970), which measures rates of water loss from leaf surfaces. Although this device measures water loss due to both cuticular and stomatal transpiration, cuticular transpiration rates were assumed to be low and were consequently ignored (see Turner et al. 1969). The instrument was calibrated under ambient conditions prior to each set of measurements, according to the procedure recommended in the instruction manual. A standard calibration plate provided by the manufacturer, with a resistance range of 3.75 s cm^{-1} to 13.7 s cm^{-1}, was used.

To investigate the possibility of differences in stomatal conductance between the upper (adaxial) and lower (abaxial) surfaces of E. incrassata leaves stomatal conductance measurements were made in the laboratory on both surfaces of leaves from E. incrassata juveniles experiencing different levels of water stress. Extensive field measurements were made on the adaxial surface of two sunlit leaves for each plant monitored. The same leaves were used for successive determinations. Diurnal courses of measurements were made for the selected groups of plants described below. Stomatal conductances were monitored during the period 23 March 1980 to 2 April 1980.

Leaf temperatures and changes in microclimate were monitored in conjunction with the stomatal conductance measurements. Leaf temperatures were recorded using the thermistor in the sensor head of the diffusion porometer. Air temperature and relative humidity readings were obtained using a standard whirling psychrometer (G.H. Zeal Ltd, London, England). Light radiation incident on the leaf was measured using a quantum sensor (Model LI-192S, Lambda Instr. Corp., Nebraska, U.S.A.) sensitive in the photosynthetically-active range of 400-700nm.

Leaf conductances and transpiration rates were calculated from the porometer measurements using the units of Cowan (1977) as described by Farquhar et al. (1978). A twelve hour light period was assumed in all cases; this was close to the actual light period on the days of measurement. Total daily adaxial conductance and transpiration were estimated using the trapezoidal rule for numerical evaluation of integrals (e.g. McCracken and Dorn 1966, pp 160-172).

5.3.3 Laboratory measurements of stomatal conductance

5.3.3.1 Methods

Differences between adaxial and abaxial conductance of leaves of E. incrassata juveniles exhibiting a range of predawn leaf water potentials were investigated under glasshouse conditions. Plants were grown from seed in 12cm diameter plastic pots and maintained under shadehouse conditions in Canberra for one year. Prior to measurement, the juveniles were moved to a glasshouse (daily mean maximum temperature 25-30°C, daily mean minimum temperature 10-15°C), and watering was discontinued after one week. Predawn leaf water potentials were subsequently measured at two day intervals to monitor the development of drought stress.

After one week a range of predawn water potentials from -0.7 MPa to -5.6 MPa had developed. Two plants were selected in each of the following stress classes: >-1.0 MPa, -1.0 to -2.0 MPa, -2.0 to -3.0 MPa, -3.0 to -4.0 MPa, <-4.0 MPa. Stomatal conductance measurements were made on the adaxial and abaxial surfaces of two leaves from each plant at 09.00 hours, 12.00 hours and 15.00 hours on two successive days. Leaf conductance was calculated for the two surfaces of each leaf for each monitoring period. The t-test for paired comparisons (Sokal and Rohlf 1969, pp 331-332) was used to compare stomatal conductances between adaxial and abaxial surfaces for each stress class. The six conductance estimates made for each leaf surface were grouped for the four leaves in each stress class.

5.3.3.2 Results and discussion

Results of the comparisons of stomatal conductance between adaxial and abaxial surfaces for the five stress classes are included in Table 5.9.

Table 5.9 Comparisons of adaxial and abaxial stomatal conductance for juveniles in five stress classes

Stress class (MPa)	df	t	P
>-1.0	23	4.336	<.001***
-1.0 to -2.0	23	.803	>.4
-2.0 to -3.0	23	1.042	>.2
-3.0 to -4.0	23	1.446	>.1
<-4.0	23	1.629	>.1

There was no significant difference in stomatal conductance between the adaxial and abaxial surfaces of leaves from juveniles of E. incrassata with predawn leaf water potentials below -1.0 MPa (Table 5.9).

For juveniles with predawn leaf water potentials above -1.0 MPa, the adaxial surfaces of leaves (mean conductance = 0.1 mol $m^{-2}sec^{-1}$) exhibited significantly higher stomatal conductances than the abaxial surfaces (mean conductance = 0.08 mol $m^{-2}sec^{-1}$). It is possible that differences in illumination between the two surfaces have a greater effect on relative conductance rates at high water potentials (e.g. see Wong 1979). For individual leaves on plants with predawn leaf water

potentials below -1.0 MPa, some variability occurred between successive monitoring periods in terms of which surface had the higher stomatal conductance. However, the differences between the two surfaces of individual leaves were almost always very small, and were also likely to be related to changes in illumination.

Adaxial surfaces of leaves exhibited higher stomatal conductances for plants with low levels of stress, and there was no difference in conductance between the two surfaces of leaves from the more stressed plants, enabling measurements in the field to be restricted to adaxial surfaces. Measuring conductances for only the adaxial surface of each leaf enabled greater numbers of leaves to be sampled and provided reliable measurements of stomatal conductance. Occasional abaxial readings were also made during monitoring of stomatal conductance in the field in order to further check differences betwen the two surfaces; any difference was almost always small. Conductances and transpiration estimates referred to in the following sections refer to adaxial surfaces only.

5.3.4 Visibly-stressed and apparently-healthy juveniles

5.3.4.1 Methods

On 23 March 1980, leaf conductances for the ten paired juveniles described in Sections 5.2.3 and 5.2.4 were monitored. Diurnal courses of measurements of adaxial stomatal conductance were made on the paired juveniles on 27 March 1980 and 1 April 1980. Predawn measurements of leaf water potential were also made on each juvenile to determine its water status (see Section 5.2.4).

On 2 April, three large, visibly-stressed juveniles and three large, apparently-healthy juveniles were selected from the group referred to above. The original paired relationships were ignored and individuals were selected to maximize differences in predawn leaf water potential. A diurnal course of measurements of both adaxial stomatal conductance and leaf water potential was made on these six juveniles on 2 April 1980.

5.3.4.2 Results and discussion

The ten visibly-stressed juveniles possessed significantly lower predawn leaf water potentials than adjacent healthy juveniles (Table 5.4). Comparisons of daily leaf conductance and daily rates of transpiration were made between the two groups of visibly-stressed and healthy juveniles (Table 5.10).

Table 5.10 Comparisons of daily leaf conductance and daily leaf transpiration between visibly-stressed and healthy juveniles for March 1980

Comparison	Mean ($mol\ m^{-2}day^{-1}$)	df	t	P
1. Daily leaf conductance:				
Visibly stressed vs	1296.00			
Healthy juveniles	3816.00	9	6.518	<.001***
2. Daily leaf transpiration				
Visibly stressed vs	22.09			
Healthy juveniles	76.32	9	6.357	<.001***

Visibly-stressed juveniles exhibited significantly lower daily leaf conductances and daily rates of transpiration than adjacent juveniles with no visible signs of stress (Table 5.10).

Diurnal courses of leaf conductance for four large and four small juveniles with leaf water deficits ranging from -0.7 MPa to -4.0 MPa are plotted in Figure 5.4. These curves demonstrate the effects of decreases in predawn leaf water potential on leaf conductance. As predawn leaf water deficits drop below -2.0 MPa, there is a tendency for a midday depression in stomatal conductance to occur. As values decrease below -3.0 MPa, the period of low conductance in the middle of the day lengthens, and eventually stomatal conductance values remain low for most of the day. Large and small juveniles appear to behave similarly.

A linear relationship was found to exist between levels of predawn leaf water potential and total daily conductance and transpiration (Figure 5.5). Regressions of these data indicated zero values of conductance and transpiration at predawn leaf water potentials close to -4.0 MPa. A plot of midday conductance and predawn leaf water potentials (Figure 5.5) indicates that values of midday leaf conductance approach zero as predawn leaf water potentials drop below -3.0 MPa. Leaf conductance estimates recalculated from the stomatal resistance measurements of Collatz et al. (1976) for seedlings of the mallee E. socialis, demonstrate a similar decrease to very low values at -3.0 MPa.

Cowan (1981) noted that "inhibition of rate of assimilation associated with decrease in leaf water content is almost invariably accompanied by reduction in stomatal aperture and rate of transpiration". A similar close relationship between rates of

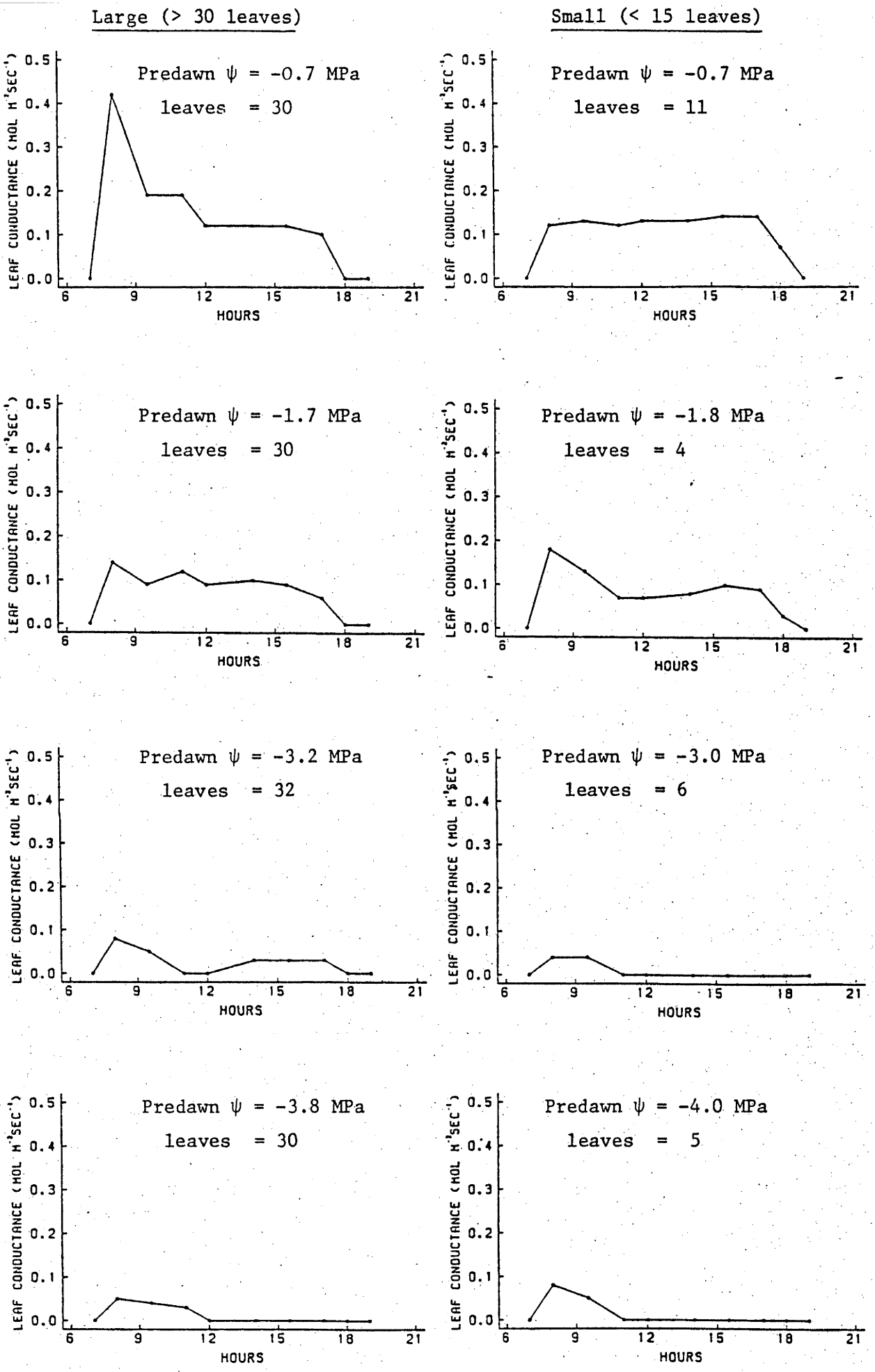


Figure 5.4 Diurnal courses of leaf conductance for large and small juveniles showing a range of predawn leaf water potentials.

transpiration, rates of assimilation, and variation in stomatal aperture has been shown to occur in a variety of Australian arid-zone species (Hellmuth 1971, Driessche et al. 1971, Doley and Trivett 1974), including the mallee E. socialis (Collatz et al. 1976). It is therefore likely that the reduction both in daily conductances and in daily rates of transpiration, observed in March 1980 for juveniles of E. incrassata with low predawn leaf water potentials, was accompanied by a decrease in carbon assimilation. The data of Collatz et al. (1976) and Wong et al. (1979) further indicate a direct proportional relationship between conductance and assimilation. The estimates of total conductance (see Figure 5.5) may thus be considered as scaled approximations to integrated daily carbon assimilation.

Measurements of stomatal conductance in the present study were made in March 1980 after local rains had resulted in a considerable increase in the low leaf water potentials measured during February 1980 (Sections 5.2.3 and 5.2.4). Most juveniles monitored in February 1980 exhibited predawn water potentials below -3.0 MPa; these juveniles would therefore have had very low leaf conductances, and reduced rates of carbon assimilation in February 1980 as a result of drought stress.

Diurnal courses of both stomatal conductance and leaf water potential for three pairs of visibly-stressed and healthy juveniles are plotted in Figure 5.6. Stressed plants demonstrated relatively little change in leaf water potential over the course of a day. The leaf water potentials of healthy plants dropped to levels similar to those exhibited by stressed plants during the day, but had largely recovered by the end of the day. Leaf conductances of healthy juveniles remained high throughout the day. In the case of one stressed juvenile, leaf conductance remained at low values for the entire day. The other two stressed plants demonstrated an early rise in leaf conductance, followed

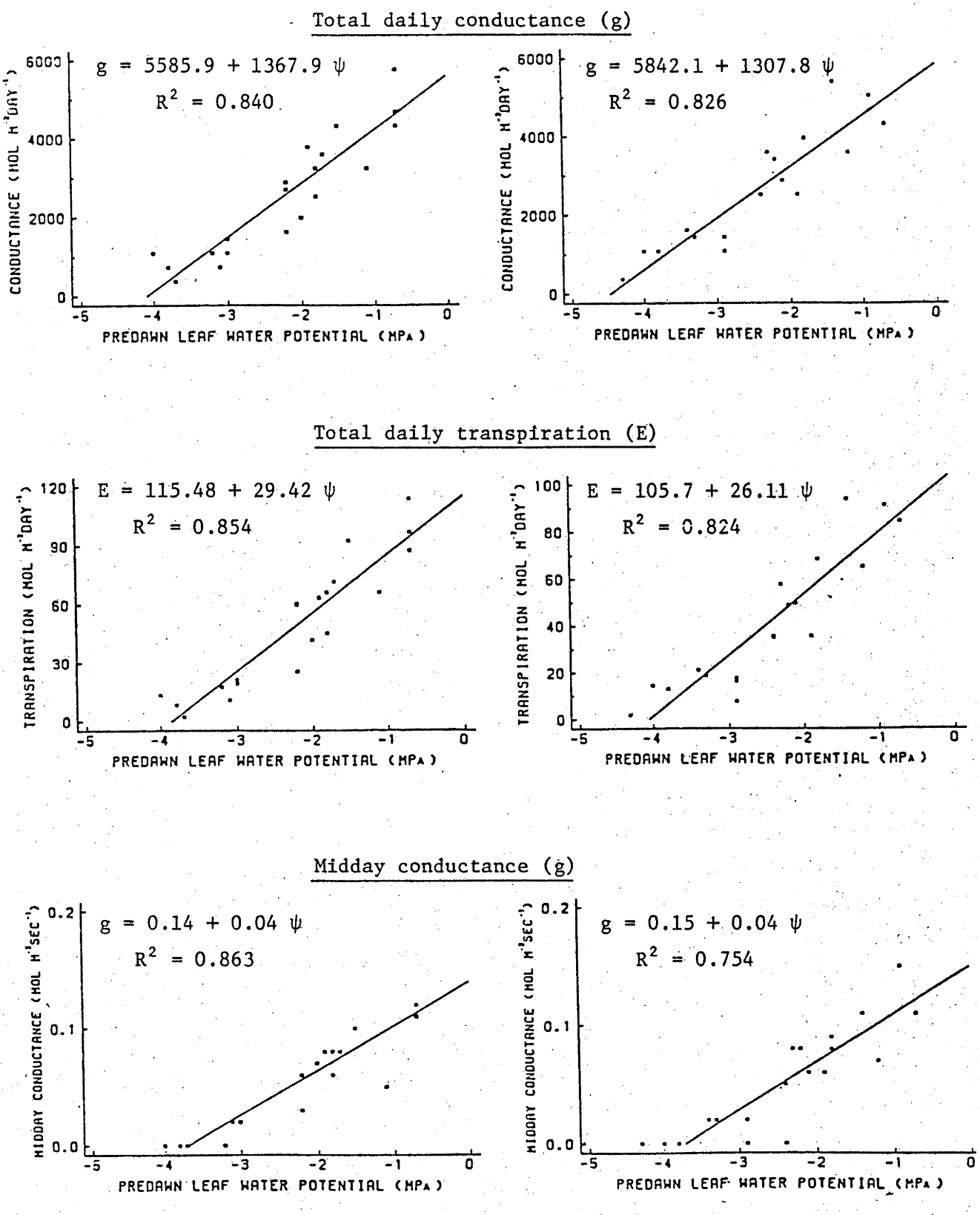


Figure 5.5 Regressions of total daily conductance (g), transpiration (E) and midday conductance (g), with predawn leaf water potential for juveniles exhibiting a range of levels of predawn leaf water potential. (n = 20)

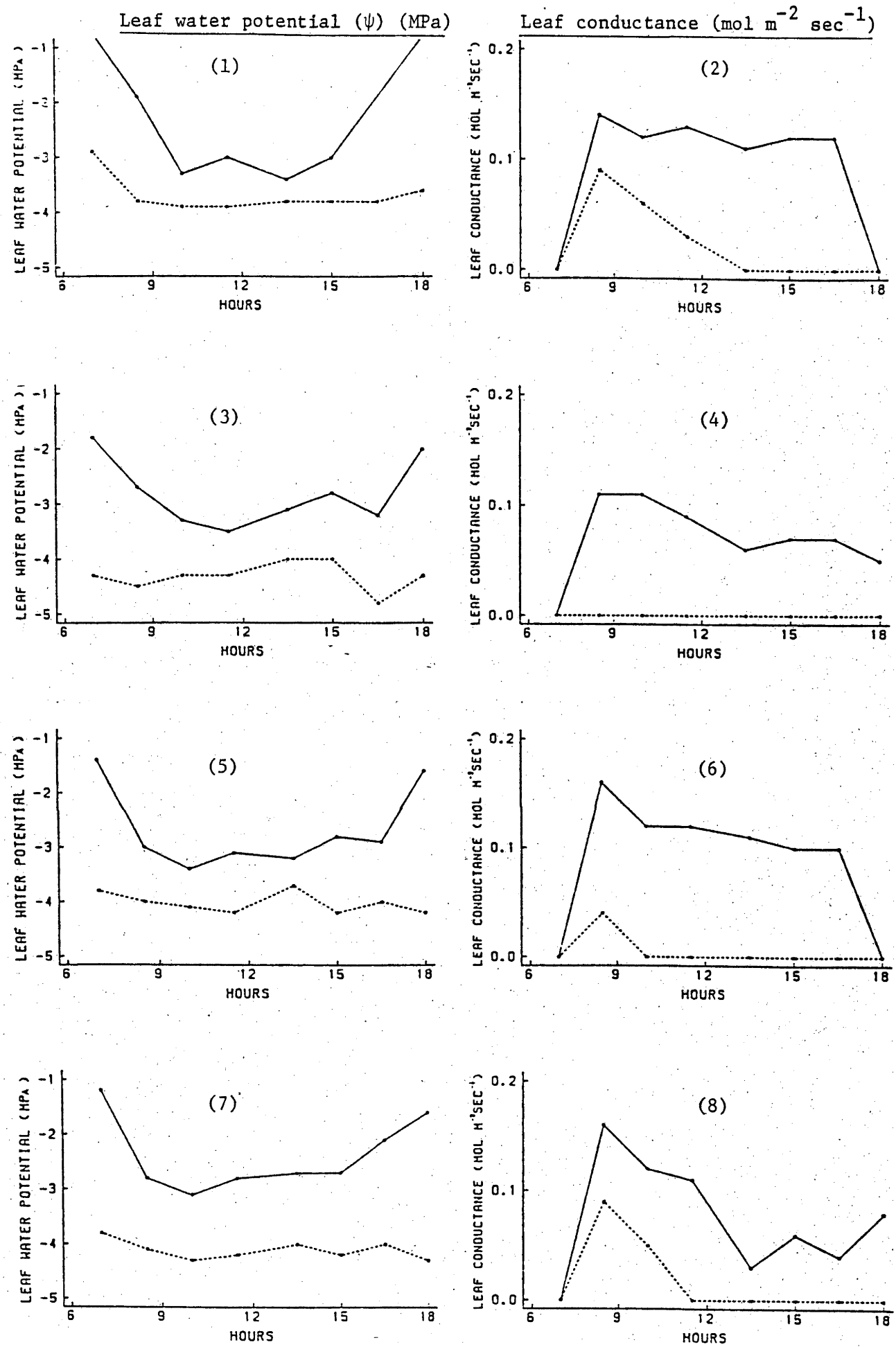


Figure 5.6 Diurnal courses of stomatal conductance and leaf water potential for three pairs of visibly-stressed (dotted lines) and healthy juveniles, (1 to 6), and stressed and healthy lignotubers (7 and 8).

by a rapid fall to low values by the middle of the day.

Drought stresses which result in low tissue water potentials and low leaf conductances are also associated with reduced rates of carbon assimilation. Juveniles of E.incrassata exhibiting visible signs of stress (i.e. leaf discoloration) have very low leaf water potentials and leaf conductances, and almost certainly have zero assimilation rates. Drought stresses are therefore likely to influence juvenile mortality both via tissue damage, and via a reduction of assimilation rates.

5.3.5 Coppicing lignotubers

5.3.5.1 Methods

In conjunction with the stomatal conductance measurements described in Section 5.3.4, another diurnal course of stomatal conductance measurements was made on a visibly-stressed and a healthy coppicing lignotuber on 2 April 1980. A diurnal course of leaf water potential measurements was also made for each coppicing lignotuber.

5.3.5.2 Results and discussion

Diurnal changes in both leaf conductance and leaf water potential for a visibly-stressed and an apparently-healthy lignotuber are shown in Figure 5.6. The responses of both leaf conductance and leaf water potential were similar to those observed in visibly-stressed and healthy juveniles.

Since the drought had broken in March 1980 it is probable that this stressed lignotuber had suffered permanent root damage, impairing water-uptake. Whether the stressed condition resulted from

drought-induced tissue damage, or from the actions of pathogenic fungi or invertebrate parasites is not known.

5.4 Summary and general discussion

Investigations described in the preceding sections show that E. incrassata juveniles may develop a low internal water status during prolonged summer droughts. The ability of juveniles to avoid low water potentials varies considerably, and plants with a wide range of predawn water potentials were found after several months of drought.

Irrigation treatments during the twelve months prior to measurement resulted in significantly higher predawn water potentials than those found in non-irrigated plants during February 1980. The greatly reduced mortality rates observed in the irrigation treatments compared to the non-irrigated controls (Section 4.5.4), together with the observed higher predawn water potentials in irrigated juveniles, shows that drought stress is closely related to juvenile mortality.

A single irrigation (20 litres each) of visibly-stressed juveniles exhibiting low predawn leaf water potentials (< -5.0 MPa) caused a significant increase in water potential to levels similar to those of surrounding, apparently-healthy juveniles. An irrigation with this quantity of water was not sufficient to fully alleviate drought stress.

A single rainfall event of ca 20 mm towards the end of a severe three-month-long drought resulted in a significant reduction in drought stress. A range of recoveries occurred as a result of the rain, and, although many juveniles were no longer stressed, some individuals remained highly-stressed. Further rainfall reduced the stress

differential in the population.

Large (>30 leaves) juveniles growing on dune crests were found to develop significantly lower predawn leaf water potentials than either large juveniles growing in adjacent swales, or small (<15 leaves) juveniles growing at both sites. Small juveniles exhibited similar predawn leaf water potentials at both sites. Large juveniles growing in swales were least stressed. The reasons for this difference are not clear, but swale soils may have a higher moisture availability than dune soils during extreme droughts. Small juveniles would therefore be disadvantaged with respect to large juveniles in swales due to smaller root systems, and competition for moisture in the upper soil strata from surrounding vegetation. Large juveniles would be disadvantaged on dunes compared to small juveniles, due to their greater evaporative surface area and the development of very low soil moisture levels at depth on the dunes.

Coppicing lignotubers were able to maintain high internal water potentials during prolonged summer droughts, when surrounding juveniles were experiencing drought stress. Low soil moisture contents of the upper soil layers apparently have little effect on leaf conductances and transpiration rates of coppicing lignotubers, indicating that these individuals have access to adequate water supplies. It is likely that coppicing lignotubers are able to draw upon moisture supplies located deep in the dunes.

Drought stress is a major factor contributing to the high mortality rates observed amongst E. incrassata seedlings and juveniles. Serious drought stresses result in tissue damage and ultimately in death. Less severe drought stresses are associated with low leaf conductances and transpiration rates, and therefore with reduced photosynthetic rates.

Prolonged reduction in carbon assimilation will significantly affect growth rates, particularly for young plants with little storage capacity.

Individuals able to avoid the development of low tissue water potentials, thereby maintaining carbon assimilation, or at worst avoiding tissue damage and death, would be at a considerable advantage. Summer drought, which is common in mallee areas, must therefore cause a strong selection pressure for the development of drought-avoidance and drought-tolerance mechanisms. Some evidence is available indicating that arid-zone species such as mallees do possess these adaptations. For example, high root/shoot ratios (Zimmer and Gross 1958), high ratios of water-supply tissue (stem) to water evaporating tissue (leaf) (Mooney et al. 1978), small leaf sizes and high specific leaf weights (Mooney et al. 1978) have been shown to occur in mallees. These are all adaptations to optimize water use efficiency. Adaptations to low tissue water potentials, including sclerophylly which minimizes tissue damage at low water potentials, and a high resilience of the photosynthetic apparatus to drought stress, also have been shown to occur in mallees (Collatz et al. 1976). Drought conditions select for individuals which possess at least some of these attributes. The high mortality rates of seedlings and juveniles which occurred during the summers of 1978/79 and 1979/80 represent this selection force in action.

CHAPTER SIX

SEED DYNAMICS

CHAPTER 6

SEED DYNAMICS

6.1 Introduction

The first three life stages in the mallee model (Figure 2.1), viz. 'flower', 'seed in fruit' and 'seed in soil', and the processes which control the movement of genets between these life stages, are collectively termed 'seed dynamics' in this thesis. The factors which control seed dynamics effectively determine the availability of genets for future recruitment into a population.

Successful recruitment of mallee eucalypts is rare, and appears to be restricted to few recently-burnt sites (Chapters 1 and 2). The question as to why recruitment does not occur more widely is as yet unresolved. An understanding of the nature of the seed dynamics of mallees may yield some insight into the factors controlling recruitment phenomena.

The present chapter briefly reviews what is presently known about the seed dynamics of mallee eucalypts and describes investigations into selected aspects of mallee seed dynamics, including:

1. storage of seed in capsules in the canopy;
2. seed drop;
3. storage of seed in the soil;
4. removal of seed from the soil.

6.2 Flowering and seed production

The periodicity of flowering in Eucalyptus species varies between individual trees, between stands of different ages, between sites, and between different species (Cremer et al. 1978). Environmental factors which are known to influence flowering include rainfall, temperature, insect damage and fire (Jacobs 1955). Rainfall is particularly important in drier areas, and Porter (1955) has demonstrated a significant correlation between high rainfall years and increased honey yields for the semi-arid, north-west of Victoria.

Although there have been no long-term phenological studies of mallee eucalypts reported, a rough estimate of flowering frequencies for some mallee species can be obtained from apiarists' records for mallee areas (see Table 6.1).

Table 6.1 Frequency of high nectar yields for six species of mallee eucalypts (obtained from Boomsma (1972) for South Australia and from Goodman (1973) for Victoria)

Species	Interval between heavy nectar yields (years)	Flowering season
E. dumosa	4	January and February
E. foecunda	2-5	December to February
E. gracilis	4-15	April to November
E. incrassata	2-5	October to April
E. oleosa	5	December to May
E. socialis	4	September to May

These records indicate that most mallee species in eastern Australia tend to flower at least once every four or five years, and that some species commonly flower more frequently. However, disruptions to flowering often occur. Drought is a feature of mallee environments and may change flowering frequencies. Heavy attacks by insects are also an occasional disruptive influence. Holland (1967) recorded total failure of a heavy flower crop of E. incrassata in Wyperfeld National Park, Victoria in 1965, as a result of widespread insect damage to developing flower buds.

Fire is a further disruptive influence affecting flowering frequencies in mallee. Fire usually kills all above-ground parts, and new stems must develop from the lignotuber before flowering can recommence. Parsons (1968) noted that little was known of the time required for mallee coppice to reach sexual maturity. In the present study, flowers were first observed on coppicing individuals of E. incrassata in August 1980, 20 months after being burned. A brief survey indicated that between 20% and 30% of coppicing lignotubers of E. incrassata would probably flower over the 1980/81 summer. Bud development appeared to be locally restricted, with some sites containing large numbers of individuals bearing buds, while other sites contained none.

Differences in flowering periods of mallee species are also evident from Table 6.1, and presumably result from genetic influences on flowering. Heavy flowering seasons were observed for E. incrassata (October 1979 to December 1979), and E. dumosa (January 1980 to February 1980) in unburnt areas adjacent to the study sites during the period 1978 to 1980. The other dominant species at the study site (E. foecunda) exhibited sparse flowering during this time, but at the end of the study period, showed indications that a heavy flower crop was

developing. Ashton (1975) noted that separation of flowering times between species is often important in maintaining their genetic integrity, and that natural hybrids may result from the overlap of flowering seasons for different species of eucalypts in a mixed stand. It appears that temporal separation of flowering times is a feature of mixed stands of mallees in the study area.

Conditions which have a negative effect on the physiological status of a plant may affect seed set as well as flowering. As a consequence, years of heavy flower crops may not necessarily result in the production of large quantities of seed. Other studies have shown that only about 10% of eucalypt ovules develop into viable seed (Cremer et al. 1978). Inadequate pollination is also an important factor limiting seed supply. Eucalypt pollen is not widely dispersed by wind (Cremer et al. 1978), and the relative abundance of pollinators, especially honeyeaters and insects such as honeybees (Ashton 1975, Bond and Brown 1979), are likely to be important in determining seed set.

6.3 Seed reserves in the canopy

6.3.1 Introduction

Many eucalypt species retain mature seed in capsules in the canopy over several years. Large variations in the amount of seed stored in the canopy are common, both between individuals in a stand, and from year to year on individual trees. Estimations of seed reserves for commercial forest trees of medium to heavy yield depend upon seed size, and may range from 1.5×10^3 to 4.8×10^5 seeds per tree, although yields of up to thirty times greater than this occur (Jacobs 1955, Cremer et

al. 1978). There are usually some trees in a stand with little or no seed reserves at any one time.

Observations made of several stands of E. incrassata at the study sites indicated large variations in the numbers of mature, intact capsules present in the canopy, both between individuals in a stand, and between stands. An attempt was made to quantify this variation.

6.3.2 Methods

A single, highly-fecund specimen of E. incrassata, selected from an unburnt stand adjacent to the burnt site in January 1980, was used to obtain an estimate of high seed loads. All intact, mature capsules on each stem were collected and counted. The capsules were air dried and the seed and chaff were removed, sieved with a 1.0 mm sieve and weighed. An estimate of the total seed load was made by counting the fully-developed seeds in ten 0.5 g random subsamples of the bulked coarse fraction. The number of seeds per capsule and the number of seeds on each stem were calculated using this estimate.

An estimate of the variability of canopy seed storage in a long-unburnt population was made by sampling individuals in a stand of E. incrassata adjacent to the burnt area. Two rectangular, half-hectare sampling areas situated about one kilometre apart, were chosen as representative of the mature mallee stands of the region. Ten individuals from each stand were selected, using random co-ordinates, in January 1980. The stems on each individual were numbered progressively in a clockwise direction and one stem was randomly chosen. All mature, intact capsules on each of the selected stems were counted. For each tree, the total number of stems, the basal diameter of each stem, and an estimate of the proportion of the canopy which had been sampled, were

recorded.

At the time the mature capsules were counted, a heavy flowering season for E.incrassata had just finished, and a large number of immature capsules were present on many of the trees. It was regarded as unlikely that the immature capsules would contain viable seed so soon (3 weeks) after flowering, and therefore immature capsules were not counted. However, by August 1980, the new capsules contained viable seed (see Section 7.3.6). In February 1981, new capsules from a further ten individuals selected from a third half-hectare sampling area, were collected and counted as described above.

6.3.3 Results and discussion

The total seed load of a large, fecund specimen of E.incrassata was estimated at 13367±2166 seeds (Table 6.2). A high variability was evident in the numbers of intact capsules per stem (mean = 860±539). This variability is also reflected in both the estimated total number of seeds per stem, and in the estimated mean number of seeds per capsule on each stem (Table 6.2). However, it should be noted that bulking the coarse sieved fraction prior to estimating the number of seeds in the 0.5g subsamples may have contributed to the variability evident in the seed estimates in Table 6.2.

The estimated total seed load, and the number of fully-developed seeds on each stem of a fecund specimen of E. incrassata are included in Table 6.2. These figures were calculated using an estimation of the mean number of fully-developed seeds per 0.5g of coarse sieved fraction (118.5±19.2 seeds).

Estimates of the variability of canopy seed storage among individuals in long-unburnt stands of E. incrassata are included in Table 6.3.

Table 6.2 Estimates of the total seed load of a large, fecund specimen of E. incrassata (January 1980) (standard deviations indicated in brackets)

Stem	No. of capsules	Wt.(g) of coarse fraction	Est. total no. of seeds	Mean no. of seeds per capsule
1	0	0	0	-
2	995	11.76	2749 (±452)	2.8
3	1329	15.23	3610 (±585)	2.7
4	442	11.74	2782 (±451)	6.3
5	1013	4.78	1133 (±184)	1.1
6	1384	12.89	3055 (±495)	2.2
Total	5164	56.40	13367 (±2166)	2.6

Table 6.3 Estimates of the variability of canopy seed reserves in long unburnt stands of *E. incrassata*

Stand	Capsule age	No. of stems sampled	Range(caps./stem) max.	min.	Mean	S.D.	Coeff. of Var.
1	pre 1980	10	1953	0	359±181	573	1.6
2	pre 1980	10	2468	5	573±257	811	1.4
3	1980	10	6665	713	2430±587	1855	0.8

A consideration of the range, the mean, and the standard deviation of the number of intact capsules per stem in each stand indicates that fecundity of stems on different individuals is highly variable in long unburnt mallee stands, and supports observations made for forest stands of other *Eucalyptus* species. Comparisons of the coefficients of variation for the three stands indicates that pre-1980 capsule loads were highly variable in both stands measured, whereas new (1980) capsule loads in a third stand were less variable. New capsules were also at least four times more abundant than old capsules in other stands. Because of sampling time differences and the fact that different stands were sampled for new and old capsules, direct comparisons of changes in fecundity as a result of the 1979/80 flowering season were not possible. However, the large increase in the mean number of capsules per stem and the decrease in variability of capsules per stem for new (1980) capsules in stand 3 implies that there was a considerable increase in fecundity following the 1979/80 flowering season.

Although no estimates of pre-dispersal predation were made in the present study, other studies of eucalypts indicate that damage by insects (Drake 1974, Boland et al. 1980), birds (Ashton 1975), and fungi (Drake 1974) may result in heavy losses of seed stored in capsules in the canopy. Observations made in unburnt E.incrassata stands during the present study indicated that pre-dispersal predation due to both birds and insects occurred, but was usually localized. No estimates of pre-dispersal predation rates were made in this study. However, other than in exceptional years, pre-dispersal predation probably does not dramatically reduce the canopy seed reserves of entire stands of E.incrassata.

It is apparent that canopy seed reserves of E. incrassata vary considerably both in space and in time. Stands which have recently flowered exhibit a higher and more uniform number of capsules per stem than stands which have not flowered for at least two years. Large variation also occurs between numbers of capsules per stem on individuals of E. incrassata. There is some evidence that numbers of seeds per capsule may also vary between the stems of particular individuals.

6.4 Seed fall and dispersal

6.4.1 Introduction

For most Eucalyptus species, release of seed from the canopy reserves follows death and desiccation of the fruits. Seed shed has been found to occur throughout the year for several eucalypt species (Cunningham 1960, Grose 1960, Florence 1964, Cremer 1965b, Christensen 1971, Ashton 1979). For most eucalypt species, rates of seed shed tend

to increase during dry periods; this phenomenon may result in seasonal variation in seed fall for species occurring in drier habitats (Cremer et al. 1978).

Seed shed commonly occurs following death of the fruits or the fruit-bearing twigs. Abscission of smaller branches is an integral part of the maintenance of canopy shape. A detailed discussion of canopy dynamics of mallee forms of Eucalyptus may be found in Holland (1969c). Fire is also an important factor stimulating seed release (Cunningham 1960, Cremer 1965b, Christensen 1971). Observations made following a fire at the study sites in January 1981 indicated that most of the canopy seed reserves were shed within one week following the fire. Similar observations have been made for E. delegatensis forests by O'Dowd and Gill (1980).

Dehiscence is accomplished via one of several mechanisms associated with desiccation and differential shrinkage of capsule tissues; these mechanisms result in widening of the locules and opening of the valves. Seed shed following dehiscence is passive and occurs largely under the influences of gravity and wind (Cremer 1965a). Most seed is shed from attached, dehiscent capsules. However, for some species, over 20% of seed fall has been found to comprise seed contained within indehiscent capsules (Cunningham 1960).

Fully-developed, fertile seeds of E. incrassata are small (1.0 mm to 2.0 mm in length) and, like most eucalypt seed, possess no special morphological features that might assist in dispersal (Boland et al. 1980). Wind is commonly regarded as the most significant dispersal agent of eucalypt seeds, although occasionally other factors such as floodwaters may be important (Jacobs 1955).

Measurements of seed dispersal in mesic and sub-alpine eucalypt forests indicate that dispersal distances are short, with most of the seed falling directly under the canopy (Cunningham 1957, Grose 1960, Cremer 1966, Harwood 1976). Cremer (1977) assessed the terminal velocities of seeds from fourteen eucalypt species covering a range of seed weights, and calculated that maximum dispersal from a forty metre high canopy in a 10 km h^{-1} wind is unlikely to exceed 40 m and is generally much less (ca 20 to 30 m). Wind speed and exposure to wind are important determinants of seed dispersal, but it has been shown that even for isolated, tall E. regnans trees, less than 30% of seed shed is dispersed distances greater than tree height (Cremer 1966).

In view of the evidence for other eucalypt species, it seems likely that seed shed from mallee crowns takes place predominantly under the canopy. In order to obtain measurements of likely maximum rates of seed shed, measurements of seed fall under fecund canopies of E. incrassata were made. At the onset of the present study, it was envisaged that measurements of seed dispersal from mallee canopies would also be made. However, practical limitations precluded these measurements.

6.4.2 Methods

Four fecund individuals of E. incrassata located in an unburnt stand on the north-west slope of a large dune adjacent to the burnt area, were selected for investigations of seed shed. Two circular seed traps, each 0.25m^2 in area, were placed under the canopy of each individual, one upslope and one downslope from the lignotuber at the base of the stems. A further two seed traps were placed in an adjacent narrow swale under an E. dumosa canopy. Both slopes leading down to the swale supported E. incrassata stands, but these seed traps were at least

10m away from the nearest E. incrassata canopy.

Each seed trap consisted of a circular, metal frame supported by metal legs at a height of about 0.8m, and from which a tapering cloth funnel with a fine mesh nylon base was suspended. The nylon base retained seed and fine chaff, but allowed rapid drainage. The lower parts of the legs were coated with a sticky substance ("Tree Tanglefoot", The Tanglefoot Co., Michigan, U.S.A.) to prevent removal of seeds by non-flying animals; these barriers were renewed periodically. The effectiveness of the tanglefoot barrier was tested by baiting the traps with lots of ten seeds: none were removed over a two week period.

The seed traps were set up in August 1979. The traps were monitored at the beginning and end of each field trip, or at two-weekly intervals in the case of longer field trips. For each trap, the numbers of 'filled' (fully-developed) seeds, 'unfilled' seeds, and mature capsules were recorded, and the presence of chaff and immature capsules was noted.

On an exceptionally windy day in early December 1979, it was found that an occasional, very strong gust of wind was capable of emptying the traps. To prevent this, the base of each trap was secured. Therefore, it is possible that the results obtained for September 1979, October 1979 and early December 1979 may underestimate rates of seed fall.

6.4.3 Results and discussion

Seed fall under fecund E. incrassata canopies occurred throughout the twelve month monitoring period from August 1979 to August 1980 (Table 6.4). The amount of seed falling varied both between individual canopies (mean seed fall = 71.4±28.6 seeds m^2yr^{-1}) and with time for

Table 6.4 Seed fall during the period 27 August 1979 to 2 September 1980

	Number of *E. incrassata* seeds per 0.5 m^2					
Monitoring time(days)	Tree 1	Tree 2	Tree 3	Tree 4	Swale	Total seeds
30	1	0	0	0	0	1
35	1	0	0	0	0	1
46	2	0	0	0	0	2
14	0	3	4	0	0	7
16	7	8	3	6	0	24
16	0	5	0	1	0	6
15	0	0	2	10	0	12
15	6	5	3	1	0	15
23	0	2	2	2	0	6
10	0	1	0	0	0	1
27	0	5	1	0	0	6
38	2	1	1	0	0	4
18	2	1	0	4	0	7
19	1	16	3	5	0	25
16	3	5	1	4	0	13
Total 373	32	55	20	39	0	146

individual canopies (Table 6.4).

Seed fall in different seasons, expressed as a percentage of the annual total (Table 6.4) indicated much higher rates of seed fall in summer (45%) and winter (33%) compared to spring (10%) and autumn (12%). The high seed fall rates which occurred during the dry summer months confirm observations made for other Eucalyptus species (see Section 6.4.1).

Some seed shed occurred as seeds enclosed in capsules. No direct estimates of this were made in the present study. Other studies have shown that the amount of seed shed of enclosed seed may be high (16% to 30% of total seed fall), but that most of this seed remains enclosed in the fruit and is therefore not an important source of regeneration (Cremer et al. 1978).

High seed fall rates also occurred during the wet winter months of 1980. It is likely that the heavy flower crop produced by E. incrassata at the study site during the 1979/80 summer influenced the seed fall rates during the following year, resulting in an increase in seed shed during winter 1980.

There were no E. incrassata seeds found in the two seed traps placed in the swale under E. dumosa canopies. A total of twenty E. dumosa seeds were recorded in these traps over the monitoring period, indicating that seed fall from the canopy also occurs throughout the year for this species.

The results presented in this section indicate that seed fall from fecund canopies of E. incrassata occurs throughout the year. Maximum rates of seed shed occur in summer, but high rates may also occur in winter. Mean rates of seed shed under fecund canopies were estimated at

ca 70 seeds m^2yr^{-2} . (Estimates on a per hectare basis are probably not meaningful considering the temporal variation in fecundity apparent in E. incrassata stands: see Section 6.3.)

6.5 Seed reserves in the soil

6.5.1 Introduction

Previous investigations of seed populations in mallee soils using either a high density flotation technique (Barbour and Lange 1966), or germination methods (Carrol and Ashton 1956, Holland 1967) have failed to detect any eucalypt seed. Studies in other eucalypt communities (Carrol and Ashton 1956, Hodgkinson et al. 1980) have found eucalypt seed occasionally present, but restricted to surface samples. High temporal variability of seed populations in soil from several eucalypt communities has been demonstrated by Barbour and Lange (1966) and Hodgkinson et al. (1980). It is possible that this variability is due to seasonal fluctuations in seed input, and a short life-span of seeds in the soil.

Although previous studies have failed to demonstrate the presence of eucalypt seeds in mallee soils, it is possible that these seeds are present in the soil only at certain times of the year. To test this hypothesis, mallee soils were collected in each season over a period of twelve months, and attempts were made to germinate seeds in the soil.

6.5.2 Methods

Mallee soil samples were collected from midslope and swale in both recently-burnt and long-unburnt stands of E. incrassata. At each location, three 0.5 x 0.5m sampling areas were selected under canopies with large numbers of capsules. Coarse litter was cleared from each sampling area and the soil was removed in layers at the following depths: 0-1 cm, 1-2 cm, 2-3 cm, 3-5 cm, 5-7 cm, 7-10 cm. Samples from corresponding depths from the three sampling areas at each location were bulked and stored in paper bags. Seed populations were determined by spreading the samples out at a depth of 2 cm in germination trays and irrigating them under glasshouse conditions (ca 20°C). Investigations of the germination behaviour of E. incrassata seeds indicated that this treatment would stimulate germination (see Chapter 7).

Samples were collected and treated in the manner described above in May 1979 (autumn) and August 1979 (winter). The same canopies were used for each sampling.

On the basis of results obtained for the initial samples (see discussion in Section 6.5.3), subsequent sampling was restricted to include only surface soil (0 to 1.0 cm depth) from unburnt stands. The area of each sample was reduced to one half of the previous size, the number of samples taken at the midslope and swale locations was increased to twelve, and the samples were taken from below six different canopies. Later samples were collected in December 1979 (spring), March 1980 (summer) and May 1980 (autumn). The samples for each location were bulked and treated as described above. All samples were retained in the glasshouse for a minimum of six months to ensure total germination.

6.5.3 Results and discussion

Soil samples collected from the area burned in December 1977 were devoid of eucalypt seed, indicating that the canopy seed reserves released onto the soil following the fire had been depleted by May 1979. Many of these seeds are known to have germinated following heavy rains in early 1978 (Chapter 4). There appears to have been no long-term storage of released seed.

No eucalypt seed was found in subsurface soil samples in either burnt or unburnt areas. The absence of eucalypt seed from the soil profile is consistent with the results obtained by other workers (Barbour and Lange 1966, Hodgkinson *et al.* 1980), and supports the view that there is no soil storage of eucalypt seed (Carrol and Ashton 1965). Surface samples from under unburnt, fecund canopies were also shown to be devoid of eucalypt seed.

Another interpretation of the above results is possible. The sampling methods used for the autumn 1979 and winter 1979 soil samples involved only three samples from each site. The sampling technique used may not have been adequate to detect seed presence in the soil, particularly if seed densities were very low, or if seed distribution was patchy. Since it was not feasible to increase the number of replicates using the previous sampling methods, it was decided to restrict future sampling to areas of unburnt stands of *E. incrassata* and to sample more widely within these areas. Other studies have demonstrated the presence of eucalypt seed on the soil surface below unburnt canopies of several *Eucalyptus* species (see Section 6.5.1). The modified sampling technique increased the chances of detecting whether this situation occurred in *E. incrassata* stands.

Results of the investigations of eucalypt seed presence in surface samples of mallee soils collected using the modified sampling technique are included in Table 6.5.

Table 6.5 Germination of E. incrassata seeds in surface samples of soil from long unburnt mallee stands (Area sampled at each site = 1.5m^2)

Season	Sampling date	No. of E. incrassata germinants	
		Midslope	Swale
Spring	December 1979	6	2
Summer	March 1980	3	0
Autumn	May 1980	1	0

The presence of germinants of E. incrassata in samples of surface soil collected in spring 1979, summer 1979 and autumn 1980 (Table 6.5) demonstrates that viable eucalypt seed is present in the soil of unburnt E. incrassata stands at certain times. The low number of germinants indicates that seed densities are low (<4 seeds m^{-2}) at any one time. The absence of eucalypt seed from the autumn 1979 and winter 1979 soil samples from unburnt areas, together with the presence of seed in later surface samples suggests either that eucalypt seed does not remain long in the soil, or that spatial variability is high and that the earlier sampling methods were inadequate. Hodgkinson et al. (1980) have demonstrated high levels of both spatial and temporal variability of E. populnea seeds in the soil; it is possible that E. incrassata seed presence in the soil is similarly variable.

6.6 Seed removal

6.6.1 Introduction

The absence of eucalypt seed from subsurface soil samples taken from eucalypt comunities (see Section 6.5.1) implies that there is no long-term soil storage of eucalypt seed. An experiment designed to investigate whether long-term soil storage of E. incrassata seed under natural conditions results in a reduction of seed viability is described in Sections 6.6 and 7.4. This experiment demonstrated that E. incrassata seed can remain buried in soil under field conditions for at least 300 days without loss of viability. Investigations of seed shed from E. incrassata canopies demonstrated a light, intermittent seed rain throughout the year (Section 6.4). The general paucity of eucalypt seeds on the soil surface, their absence from the subsurface soil despite a continual input of seeds onto the soil surface, and a demonstrated ability to survive burial for at least one year, indicate that factors other than supply and storage limitations may influence seed reserves in the soil.

Removal of seeds by seed harvesting ants has been shown to occur in E. regnans forests (Ashton 1979). Jacobs (1955 p 109) has shown that treatment of plots with insecticide prior to sowing with E. cinerea seed may result in good germination up to eighteen months after sowing, compared to zero germination in adjacent control plots. Cremer et al. (1978), in summarizing studies on several species of Eucalyptus, noted that up to 80% of eucalypt seeds in the soil are destroyed by insect predators such as ants and lygaeid bugs. It therefore seemed likely that insect seed predators are important in reducing the number of viable eucalypt seeds present in mallee soils.

The importance of seed harvesters in desert ecosystems has been recently reviewed by Brown et al. (1979) who noted a high diversity of granivorous ants in Australia when compared to other continents. Studies in arid areas (Morton 1980) and semi-arid areas (Briese 1974, Briese and Macauley 1981) highlight the importance of the role played by ants in removing seed from the soil surface in several plant communities.

In the present study, an attempt was made to assess the importance of predators, particularly seed harvesting ants, in removing E. incrassata seed from the soil surface. A series of experiments were set up to determine:

1. whether E. incrassata seeds are removed from the soil surface;
2. rates of seed removal;
3. temporal and spatial variation in removal rates;
4. whether the addition of large amounts of seed at high densities results in soil storage of seed.

These experiments are described in the following sections.

6.6.2 Measurements of rates of seed removal

6.6.2.1 Introduction

Ashton (1979), in an investigation of seed removal from the soil surface in E. regnans forests, used baits of fully-developed eucalypt seeds placed in specially cleared sites on the forest floor. Rates of removal were measured by monitoring the number of seeds remaining at each site at periodic intervals. An approach similar to this was adopted in the present study.

6.6.2.2 Methods

To determine whether ants were responsible for removing seed from the soil surface, baits consisting of ten, fully-developed E. incrassata seeds placed along a line at 1cm intervals were set up in two areas of unburnt mallee several kilometres apart. The baits were set up in early December 1979 and observations were made at each site for ten minutes every two hours over a sixteen hour period. At both sites, ants were observed removing seeds from the baits and carrying them into nest entrances leading below ground.

In order to quantify removal rates, a transect of five permanent baiting quadrats was set up at one of these sites. Each quadrat comprised a circular area of 1m radius. The quadrats were located at 10m intervals along a transect line. Baits of ten seeds (see above) were set up in the quadrats in the early morning (prior to 10.00 hours). A single bait was set up in each quadrat on each of three consecutive days; the baits in each quadrat were separated by at least 1m. The number of seeds removed from each bait was monitored in the early morning and at dusk for the duration of each field trip. Measurements commenced in December 1979 and were repeated at approximate monthly intervals until August 1980.

A similar transect was established in the recently-burnt area approximately 1km away from the unburnt monitoring site, and was used to monitor seed removal from the soil surface of recently-burnt sites during February and March 1980.

6.6.2.3 Results and discussion

A summary of percentage seed removal data for the unburnt site is shown in Table 6.6. For each monitoring period, seed removal data for each quadrat were pooled, and the numbers of seeds removed for each day of exposure were expressed as a cumulative percentage of the total 150 seeds.

Table 6.6 Cumulative percentage seed removal from baited areas in an unburnt E. incrassata stand (n=150)

	1979			1980					
Days exposed	Dec	Jan	Feb	Mar	Apr/May	Jun	Jul	Aug	Mean
1	73	62	58	78	78	67.3	95.3	76.7	73.5
2	89	76.7	68	91.3	90.7	82.6	96	98.7	86.6
3	97	86.7	72.7	92.6	90.7	87.9	96.7	100	90.5
Total	100	90	92	93.3	90.5	100	100	100	
No. of days monitored	4	6	16	8	5	11	7	3	

Rates of seed removal from the baiting stations were consistently high over the nine months of monitoring, with more than 90% of E. incrassata seeds being removed by the end of each monitoring period.

Most seeds (>70%) were removed during the first three days following exposure, with the highest removal rates consistently occurring during the first twenty-four hours of exposure.

The total number of seeds removed during day and night for the first three days of exposure in each of the three monitoring periods in summer (December 1979 to February 1980), and in winter (June to August 1980), are included in Table 6.7

Table 6.7 Diurnal and nocturnal seed removal after three days exposure in summer 1979/80 and in winter 1980 (unburnt sites) (n=450)

	Number of seeds removed	
Period	Summer	Winter
Day	58	419
Night	326	8
Total	384	427

A comparison of seasonal differences in the total number of seeds removed (out of a possible 450 seeds) after three days exposure on the soil surface, indicated significantly higher seed removal rates in winter ($X^2_{(1)} = 23.056$, $P<.001$***) (Table 6.7). Most seeds were removed during the night in summer, and during the day in winter. Diurnal and nocturnal rates of seed removal were significantly different, both within seasons and between seasons (e.g. initial 3 days exposure in

summer: day vs night comparison, $X^2_{(1)} = 187.042$, P<.001***). During autumn, time constraints restricted monitoring of seed removal to once every twenty-four hours (09.00-10.00). As a result, day/night comparisons were not possible for this season.

Ants observed removing eucalypt seeds from baits during the course of the study were identified (see Table 6.10). Changes in taxa were found to occur in association with the observed seasonal changes in daily harvesting activity. Similar seasonal changes have been observed both in daily activity patterns and in species composition in other studies (Briese 1974, Davidson 1977, Ashton 1979, Andersen 1980). These changes are apparently influenced by a variety of factors including temperature, moisture, light intensity, food availability and interspecific competition (Briese 1974, Briese and Macauley 1980). The changes are believed to reflect physiological and morphological adaptations which facilitate foraging, rather than a temporal partitioning of resources (Brown et al. 1979).

Removal rates of E. incrassata seeds from baits placed in the recently-burnt area in February 1980 and March 1980 were similar to rates measured in the adjacent unburnt area (Table 6.8).

Table 6.8 Cumulative percentage seed removal from the soil surface of a recently-burnt and a long unburnt stand of E. incrassata (n=150)

Days exposed	Burnt		Unburnt (from Table 6.6)	
	Feb 1980	Mar 1980	Feb 1980	Mar 1980
1	48	84	58	78
2	58.7	92.7	68	91.3
3	68	95.4	72.7	92.6
Total	76	95.4	92	93.3
No. of days monitored	6	8	16	8

With the unlikely exception of some long-distance dispersed seed, there is unlikely to have been any eucalypt seed input into the burnt area once seed shed from the burnt canopies had ceased. The seed harvesting component of the ant fauna had apparently either recovered from the effects of the December 1977 fire by February 1980, or else had suffered little effect as a result of the fire. Work by Majer (1980) favours the latter explanation. Presumably these species are generalist seed harvesters, and are able to find other food sources in the absence of eucalypt seed. The low total number of seeds removed from the burnt sites in February 1980 probably resulted from the shorter monitoring

time for this site, compared to the unburnt site.

A detailed investigation of the ant fauna of a dune site located several kilometres south of the sites in the present study has been conducted by Andersen (1980). Andersen's study, which commenced in January 1980, also found removal rates of Eucalyptus seed that were similar between unburnt and recently-burnt sites. However, seed removal rates measured by Andersen in February 1980 and June 1980, were generally lower than those measured in the present study. This difference may have resulted from Andersen's technique of including seeds from three different Eucalyptus species in each bait. Site differences in ant fauna may have also been important.

In summary, ants remove E. incrassata seeds from the soil surface of both unburnt and recently-burnt stands of mallee. Removal rates are high (>90%). Most of the seed (>70%) is removed in the first three days of exposure. Removal is predominantly nocturnal in summer and diurnal in winter. Different species are active in different seasons. Significantly higher removal rates occur in winter.

6.6.3 Spatial and temporal variations in seed removal

6.6.3.1 Introduction

Different rates of seed removal from baits separated by distances as small as 1m were observed during the course of the experiment described in Section 6.6.2. It therefore seemed likely that the survival chances of a seed landing on the soil surface might vary considerably within a small area. It was also apparent from the investigations described in Section 6.2 that seed densities occurring

under conditions of natural seed fall are generally much lower than those used in the baiting quadrats of the previous experiment.

An experiment was set up to investigate spatial patterns of seed removal activity. Isolated seeds were used as baits in order to relate the removal rates measured to likely natural seed densities occurring in unburnt stands of mallee.

6.6.3.2 Methods

A 20m x 10m grid marked with wire pegs at 2m intervals was established in February 1980 in an unburnt stand adjacent to the transect described in Section 6.6.2. A single, fully-developed seed was placed close to the base of each peg on the grid. Where pegs were situated in heavy litter, a small area of about 5cm diameter was cleared of litter and the seed placed in the cleared space; this allowed relocation of the seed with a minimum of disturbance.

Each of the sixty-six points within the grid were monitored daily, usually between 09.00 hours and 10.00 hours, and the points from which seeds had been removed during the previous twenty-four, hour period were recorded. Seeds removed were not replaced. Monitoring of removal rates from the grid commenced in February 1980, and the experiment was repeated monthly until August 1980.

On two occasions heavy showers of rain caused some doubt as to whether seeds which could not be relocated on that day had disappeared as a result of harvesting activity, or from rain splash. Only small numbers of seeds were involved in each case. The few missing seeds were replaced with new seeds, and it was assumed that no removal had occurred on these two days. The removal rates for the monitoring periods in June 1980 and August 1980 may therefore represent slight underestimates.

Seeds were easily relocated on most occasions and there appeared to be no movement of seed as a result either of surface wind effects, or from the several light showers of rain encountered during the monitoring periods.

6.6.3.3 Results and discussion

Rates of seed removal from the grid were expressed as cumulative percentages of the total sixty-six seeds for the initial three days of exposure and are included in Table 6.9.

Table 6.9 Cumulative percentage seed removal from the baiting grid located in an unburnt *E. incrassata* stand during 1980 (n=66)

Days exposed	Feb	Mar	Apr/May	Jun	Jul	Aug	Mean
1	30.3	37.9	45.5	40.9	69.7	34.9	43.2
2	42.4	43.9	57.6	53.0	77.3	40.9	52.5
3	43.9	48.5	65.2	63.6	77.3	54.6	58.9
Total	66.7	65.2	65.2	86.4	84.9	89.4	
No. of days monitored	7	8	3	12	9	15	

A comparison of the total percentage seeds removed after three days exposure between the grid (Table 6.9: isolated seeds) and the transect (Table 6.6: seed caches) over the period February 1980 to August 1980 was made using normalized percentage data. Isolated seeds were removed at significantly lower rates during the first three days of exposure than seed in caches of ten ($t_{(5)} = 4.618$, $P<.01$**). It appears that seed harvesters were more likely to locate and remove seed from caches.

Efficiency of seed removal by ants apparently varies between different species, and is thought to depend both on foraging strategies and on seed density (Brown et al. 1979). Foraging strategies have been broadly divided into group and individual strategies. Group foragers are believed to be more efficient at reducing high seed densities whereas individual foragers are able to utilize seed resources at densities too low to be profitably exploited by group foragers (Davidson 1977). In the present study, identification of the ants observed removing seeds from monitoring areas was carried out to generic level, and probable foraging strategies for these genera were obtained from Morton (1980) (see Table 6.10).

Table 6.10 Types and probable foraging strategies of ants observed harvesting E. incrassata seed at the study sites during 1980.

Genus	Foraging strategy	Season collected
Meranoplus	individual	summer
Chelaner	group	autumn/winter
Monomorium	group	autumn/winter
Rhytidoponera	individual	winter

Both group and individual foragers were present at the monitoring sites. Studies of other areas have also demonstrated the presence of both types of foragers (Briese 1974, Morton 1980, Andersen 1980). It should be emphasized that no systematic collection of seed harvesting species was attempted in the present study and therefore the list presented in Table 6.10 is not exhaustive, particularly for the summer season. Andersen (1980) has made detailed collections of ant species in the study area. In view of the theories put forward by Davidson (1977) concerning relative efficiencies of foraging strategies in relation to seed densities (see above), the increased removal rates of seeds from caches may be due to a high proportion of group foragers.

A comparison of seasonal differences in the number of isolated seeds removed from the grid during the initial three days of monitoring in summer/autumn (February and March 1980) and in winter (July and August 1980), indicated that significantly more seeds were removed in winter than in the warmer months ($X^2_{(1)} = 13.462$, $P<.001$***).

Figure 6.1 Spatial variation in mean survival time (days) of isolated *E. incrassata* seeds (Grid interval = 2m) (February 1980 to August 1980)

0	0	3	3	4	2	0	3	1	5	1
1	5	0	2	3	1	4	5	7	5	3
4	6	4	4	5	2	1	2	2	8	0
6	5	2	7	2	2	0	0	7	6	5
1	5	6	7	3	3	2	2	10	2	5
2	5	6	3	3	3	0	5	10	7	5

Seed removal rates were found to vary considerably between sites in the grid. The mean survival time of an isolated seed was calculated for the six seeds placed at each point in the grid during the six monitoring periods. When a seed was not removed by the end of monitoring, or if it survived more than ten days, the it was assigned a value of ten. The mean survival time for isolated seeds placed at each point in the grid is shown in Figure 6.1.

A high variability in removal rates between sites separated by 2m is evident from a consideration of Figure 6.1. Sites of very rapid removal (mean survival time <1 day) were adjacent to sites of low removal rates (>7 days). Some sites appeared to be subject to no seed harvesting activity at all. Spatial variability of seed removal activity is high when measured at a resolution of 2m and it is possible that the scale of variation is even finer. Isolated seeds landing on the soil surface are thus likely to have very different survival chances, depending on the site at which they land. Presumably some seeds landing in regions of low removal activity may find safe sites and therefore result in a very sparse, patchy seed storage in the soil.

Seed shed from the canopy of an unburnt, fecund specimen of E. incrassata occurs as a light, intermittent seed rain throughout the year (Section 6.4). Seed densities on the soil surface at any particular time are likely to be very low, with the majority of newly-fallen seeds occuring as isolated seeds rather than in caches. Removal rates of naturally-fallen seed are therefore probably similar to the removal rates measured for isolated seeds using the grid described above. The mean percentage removal of isolated seeds from the grid for the first twenty-four hours of exposure to seed harvesters was calculated from Table 6.9 as 43.2%. The half-life of an isolated seed on the soil surface was calculated from removal data collected during

the period February 1980 to August 1980 for 396 seeds as ca 1.7 days.

Harvesting of seeds from the soil surface is obviously an important factor limiting soil storage of E. incrassata seed. Seed harvesters are capable of removing at least 70%, and probably up to 90-100% of newly-fallen seed. Seed removal is rapid, and therefore the chances of significant amounts of seed finding 'safe' sites (e.g. below the soil surface as a result of soil disturbance by animals) will be low. However removal rates were shown to be spatially variable and areas of consistently low harvesting activity occurred. It therefore seems that low density, patchy soil storage of E. incrassata seed is possible.

6.6.4 High seed densities and seed removal

6.6.4.1 Introduction

The restriction of successful recruitment of mallee eucalypts to recently-burnt sites, together with a general absence of eucalypt seed populations in the soil in unburnt stands, suggests that fire is an effect which may result in the establishment of seed populations in the soil. Similar recruitment patterns have been observed for many species of Eucalyptus. In the case of fire-sensitive ash species (i.e. E. regnans, E. delegatensis), these observations have led to speculation that fire-induced synchronous release of all canopy-stored seed results in the 'satiation' (Janzen 1969) of seed predators thereby allowing seeds to find 'safe' sites in the soil (Ashton 1979, O'Dowd and Gill 1980).

Predator satiation occurs when predator populations are unable to respond to rapid fluctuations in food supply (Janzen 1969, 1971). The lag in predator response increases the time for which seeds remain on the soil surface, and therefore larger numbers of seeds may either germinate or shift into sites safe from predators. The satiation phenomenon, associated largely with annual variations in the amount of seed produced, has been observed for a number of northern hemisphere plant species (Watt 1923, Janzen 1971). Simultaneous release of large quantities of seed from canopy reserves, as occurs in Eucalyptus species following fire, is likely to produce a similar effect.

The following experiment was designed to test the hypothesis that sudden, massive release of eucalypt seed onto the soil surface results in an increase in soil storage of eucalypt seed. Seed was distributed over the soil surface in an unburnt stand of mallee at densities thought to be similar to those associated with natural seed release following fire. Seed populations in the soil were monitored subsequent to seed addition.

6.6.4.2 Methods

The total seed load from a large, fecund specimen of E. incrassata was collected. Estimations indicated that the seed load was ca 1.3×10^4 seeds (see Section 6.3). Dispersal distances of eucalypt seeds are believed to be short, with most of the seed falling below the canopy (Section 6.4). Calculations of likely seed densities below a 4m high mallee carrying 1.3×10^4 seeds indicated a density of ca 260 seeds m^{-2} if all the seed was dropped uniformly in an area with a radius equal to canopy height, and a density of ca 65 seeds m^{-2} for a radius of twice canopy height.

Two concentric, circular quadrats of radii 3m and 7m were established, largely under canopy, in an unburnt stand of E. incrassata in February 1980. Seed and chaff collected from the tree mentioned above were broadcast by hand at densities of ca 300 seeds m^{-2} in the inner circular quadrat, and ca 50 seeds m^{-2} in the outer annular quadrat. In order to achieve an even distribution, the quadrats were subdivided into quadrants, and appropriate amounts of seed and chaff were scattered separately onto each section. Fine chaff was included to mimic natural seed release.

To monitor seed presence in the soil, samples of soil were collected at intervals of zero, one, two, four, eight, twenty-eight, sixty, 120, 150 and 200 days following seed addition. For each quadrat, eight subsamples of surface soil totalling $0.25m^2$ were collected at each monitoring interval; two subsamples were located in each quadrant. Soil was collected to a depth of 1cm. Areas from which samples were taken were marked to prevent resampling. The germination methods described in Section 6.5.2 were used to detect the presence of viable seed.

The effect of 'in situ' soil storage on seed viability was monitored in parallel with the experiment described above. Twenty $0.25m^2$ quadrats, each containing 100 buried E. incrassata seeds were established on the same day, and in the same stand as the two circular quadrats containing surface-added seed. The batches of one hundred seed were buried at about 1cm depth. Soil to a depth of ca 1.5cm was collected from two of these quadrats at each of the monitoring intervals referred to above, and additionally at 300 days, and treated as described in Section 6.5.2. A total of $0.5m^2$ of surface soil comprising sixteen subsamples were also collected from areas adjacent to the quadrats in order to monitor natural input of seed from the trees in the

stand.

6.6.4.3 Results and discussion

A summary of the germination data for soil samples from quadrats with surface-added seed and buried seed, and from surrounding 'control' areas is presented in Table 6.11.

It is apparent from Table 6.11 that, following the addition of large quantities of eucalypt seed to the soil surface of an unburnt mallee stand, seeds remained present in the soil at densities of greater than 4 seeds m^{-2} for at least 60 days. Laboratory germination rates of E. incrassata seeds added to soil were determined to be ca 47% (Section 7.2.2). It is therefore possible that actual seed presence may have been up to twice as great as the number of germinants detected in the samples.

The germination rates obtained for buried seed demonstrated a small but statistically significant decrease in viability for storage times greater than twenty-eight days, compared to zero storage time (see Section 7.3.6). Consideration of the variability evident in samples with storage times between twenty-eight days and three hundred days (95% confidence limits = 37 ± 7) indicated no significant changes in viability during this storage period. Thus the decrease in the number of germinants observed in soil samples taken from the quadrats with surface-added seed is unlikely to have been caused by loss of seed viability associated with soil storage. Germination data for the control samples indicates that an occasional viable seed was present in the soil, but that input of seeds from natural seed fall was unlikely to have influenced the results.

Table 6.11 Numbers of germinants in $0.25m^2$ soil samples taken from quadrats with surface-added seed and buried seed, and from surrounding 'control' areas. (n=100) (Percentage germination is indicated in brackets)

Days exposed	Surface-added seed		Buried seed+	Controls
Density of added seed (per $0.25m^2$):	75 (estimated)	12.5 (estimated)	100 (actual)	0
0	23 (31)	7 (56)	54	0
1	10 (13)	11 (88)	N	N
2	15 (20)	5 (40)	N	N
4	13 (17)	0 (0)	N	N
8	12 (16)	2 (16)	N	N
28	6 (8)	3 (24)	21	0
60	1 (1)	1 (8)	40	0
120	1 (1)	0 (0)	33	1
150	0 (0)	1 (8)	39 ± 13++	0
200	0 (0)	0 (0)	40	0
300	N	N	35	0

Notes: + Mean of 2 replicates, each 100 seeds .25m

++ Mean $\pm$ S.D. of 6 replicates: all field germination

N = zero samples taken

From the evidence presented in previous sections of this chapter, it seems that seed removal by harvester ants was an important factor contributing to the observed depletion of soil seed reserves. A number of factors render a detailed analysis of seed depletion rates difficult to achieve. Initial seed densities are unlikely to have been uniform at the scale used for sampling, despite the sowing techniques used. Heterogeneity in removal activity is also likely to have occurred over short distances (<2m) in the quadrats (Section 6.6.3), thus increasing variation in seed densities and necessitating high sample replication to obtain reliable seed density estimates. Changes in seed germination in samples due to soil factors is a further source of possible variation.

Soil samples with surface-added seed, which were collected at day zero, exhibited high seed densities for both quadrats (Table 6.11). Samples collected during the first twenty-eight days of exposure showed high variations in seed density. Spatial heterogeneity of removal activity is likely to have caused variations in seed density during this early period, and may have contributed to the observed variation in germination data. By sixty days following seed addition, the number of germinants in high and low density areas had been reduced to similar densities (ca 4 seeds m^{-2}). Seeds were present in soil samples up to 150 days following seed addition, but no seeds were detected in samples collected at 200 days.

Greater numbers of seeds were removed from the high density quadrat than from the low density quadrat in the period up to sixty days exposure (Table 6.11). Two possible factors which may have contributed to increased removal rates in high density areas are: a 'functional' response by predators in which the number of seeds removed by individual seed harvesters increases due to the greater ease with which seeds in high density areas can be located; and a 'numerical' response in which

the density of predators increases due to the increase in food resources (Holling 1959).

Although no information was collected on changes in predator densities as a result of the seed input to the quadrat areas, the time lag between addition of seed and its depletion to low densities (between 28 days and 60 days) implies that any numerical response of predators is slow. Early seed depletion is therefore probably largely due to a functional predator response. The lower rates of removal from the low density area may result from the fact that seeds are harder to find. In this case, rates of removal would probably decrease with reductions in seed density in both quadrats until seed densities of the two quadrats approached similar levels. This situation appears to have occurred by sixty days after seed addition (Table 6.11).

It seems likely that some of the seeds remaining in the quadrats after sixty days had shifted into 'safe' sites below the soil surface. The effects of animals (e.g. kangaroos and litter-foraging birds) in disturbing the soil surface may facilitate the shifting of seeds into the soil. Great care was exercised in minimizing soil disturbance to the quadrats during monitoring.

Conditions during the period April 1980 to August 1980 were apparently favourable for germination of eucalypt seed, and resulted in field germination of both surface-added seed and buried seed in the quadrats. Field germination in these quadrats is discussed more fully in Section 7.4. The fact that germination of seeds in the quadrats continued until August 1980 further indicates that, following seed release, seed may be stored in the soil for up to 200 days.

The mean field germination rate observed in quadrats containing 100 buried seeds was 39±12% (see Table 6.11). A total of eighty-four field germinants were detected in the quadrats containing surface-added seed by the end of August 1980. Twenty-four field germinants were located in the inner (high density) quadrat, and sixty germinants in the outer (low density) quadrat. The similarity of field germination densities in both quadrats (inner:outer = 1.8:1), when compared to the initial densities of dispersed seed (inner:outer = 6:1) confirm that removal rates must have been initially higher in the high density, inner quadrat, and that differences in removal rates eventually resulted in similar seed densities in both quadrats.

In summary, it appears that addition of large quantities of E. incrassata seed onto the soil surface of an unburnt stand of E. incrassata at densities thought to be similar to those resulting from natural seed shed following fire, may result in soil storage of eucalypt seed for periods of at least 200 days. Buried seed exhibits a small but significant initial loss of viability as a result of soil storage, but no further viability losses occur for storage periods of between twenty-eight and 300 days. Seed added to the soil surface is depleted, and rates of depletion appear to be density dependent with higher seed removal rates occurring in areas of higher seed densities. The difference in removal rates eventually results in similar seed densities in both areas. When the appropriate field conditions arise, field germination of both buried seed and surface-added seed occurs. Field germination rates of buried seed are similar to laboratory germination rates of seed in soil.

The occurrence of field germination in the quadrats during the period April 1980 to August 1980 occurred following massive seed input during February 1980. The timing of these events is similar to

situations which occur naturally, and thus indicates that natural soil storage of seed is possible for periods sufficiently-long for recruitment to take place.

6.7 Summary and general discussion

Flowering and seed set are highly variable in mallee eucalypts, including E. incrassata. An underlying periodicity of two to four year intervals between years of heavy flowering exists, but may be modified by environmental factors, particularly drought, fire and insect damage. Seed set is dependent on other factors such as abundance of pollinators, and may occur less frequently than flowering.

Seed is stored in capsules in the canopy. The amount of seed stored exhibits high spatial and temporal variability. Seed shed occurs passively following capsule death, and may occur at low rates throughout the year when associated with natural capsule death, or at high rates over a short period as a result of fire. Rates of seed fall beneath unburnt, fecund E. incrassata canopies were estimated at ca 70 seeds per year.

There appeared to be no seed reserves stored at depth in the soil in unburnt stands. However, viable E. incrassata seeds occasionally occurred on the soil surface at very low densities. It is likely that seed presence in the soil in unburnt stands is highly variable, both spatially and temporally. E. incrassata seed rapidly disappeared from the soil surface of both long-unburnt, and recently-burnt stands. Seed harvesting ants were observed removing seed from baits. Removal rates were high, with >90% of seed removed from caches and >70% of isolated

seeds removed from the soil surface during monitoring times. The half-life of an isolated seed on the soil surface of an unburnt stand was calculated at ca 1.7 days.

Seed removal was predominantly nocturnal in summer and diurnal in winter. Different ant species were active in different seasons. Removal rates were high over all seasons, but winter removal rates were significantly higher than summer rates. Seed was removed more rapidly from caches, and from areas where it was added at high densities, than from low density areas., This phenomenon may be due to differences in foraging strategies. Both group foragers and individual foragers were active in the same areas.

Spatial variation in seed removal activity (measured for isolated seeds) was high with areas of consistently low removal rates situated as close as 2m from areas of high removal rates. Observations made of seeds in caches indicated that this variation may occur over distances of less than 1m. Areas exhibiting zero removal rates also occur and may facilitate some low density soil storage.

The addition of seed to the soil surface of unburnt stands at densities which may occur following the simultaneous release of all canopy seed reserves resulted in the establishment of seed reserves in the soil for periods of at least 200 days. Buried seed exhibited little loss of viability over periods of up to 300 days soil storage. It is likely that significant seed reserves in the soil may occur as a result of the inability of seed harvesting ants to respond to a sudden massive increase in food supply. This phenomenon is similar to the 'predator satiation' condition described by Janzen (1969).

Seed removal from the soil surface is obviously an important factor limiting the establishment of significant E. incrassata seed reserves in the soil of unburnt stands. A light seed rain occurs from fecund canopies throughout the year, and areas of low or zero removal activity occur, thus indicating that isolated seeds may occasionally escape from seed harvesters and remain in the soil in unburnt stands.

Although eucalypt seed cannot remain dormant for long periods under natural soil conditions (Cremer et al. 1978), the seeds of some species have been shown to remain viable in the soil for periods of up to two years (Jacobs 1955, Cunningham 1960), and for up to 300 days in the case of E. incrassata. Conditions suitable for germination probably arise in most years in mallee environments. However, despite the likely presence of some seed in the soil of undisturbed stands, E. incrassata seedlings have never previously been reported as occurring in undisturbed situations.

Field germination of both buried and surface-sown seed occurred during the autumn and winter seasons following the addition of seed to the soil in late summer 1980. It appeared that there were no soil factors inhibiting germination of seeds at this site. This was confirmed to be a general phenomenon with the discovery of widespread natural germination of E. incrassata seeds in unburnt mallee stands during winter 1980 (see Section 7.2.2). However, none of the new germinants survived beyond the beginning of summer 1980/81. Thus it is likely that the apparent absence of seedlings from unburnt mallee stands is due to the inability of newly-germinated seedlings to establish successfully. The tendency for successful recruitment to be restricted to recently-burnt situations may therefore result both from the creation of large seed populations in the soil due to predator satiation following fire-induced mass seed release, and to the development of

conditions suitable for seedling establishment in recently-burnt areas. The combination of seed removal by ant harvesters and the infrequency of suitable establishment conditions in unburnt situations may effectively preclude recruitment in unburnt stands.

CHAPTER SEVEN

GERMINATION BEHAVIOUR

CHAPTER 7

GERMINATION BEHAVIOUR

7.1 Introduction

The significance of seed harvesting by ants in removing most of the Eucalyptus incrassata seed that falls onto the soil surface was discussed in the previous chapter. Investigations show that seed may escape being harvested, either by landing in an area of low harvester ant activity (see Section 6.6.4) or by being buried (Section 6.6.5). This seed may germinate if suitable conditions arise (Section 6.6.5.2).

The absence of E. incrassata seedlings from long-unburnt sites, despite the occasional presence of seed in the soil (Section 6.5), suggests that either the conditions necessary for germination seldom arise, or that newly-germinated seedlings are unable to establish at these sites. The rarity of seedling recruitment in recently-burnt areas (see Chapter 1), despite the likelihood of the presence of large seed populations in the soil for some time after the fire (Section 6.6.5), further indicates that absence of seeds from the soil is not solely responsible for the observed paucity of mallee seedling recruitment.

In order to investigate the role that germination behaviour plays in the recruitment of mallee genets, investigations into the germination responses of E. incrassata seeds were carried out. The present chapter describes investigations of particular germination properties of E. incrassata seeds, including:

1. germination rates of seeds placed on moist filter paper ;

2. germination rates of seeds sown in soil and irrigated under glasshouse conditions;
3. germination rates of seeds sown at different depths in soil;
4. germination rates of seeds buried in soil in the field;
5. the effects of light and temperature on germination;
6. the effects on germination of specific factors associated with fire (viz: soil heating, litter removal, ash addition);
7. the effects on germination of storage of seed under laboratory conditions;
8. the effects on germination of storage of seed in soil in the field.

7.2 Germination rates

7.2.1 Laboratory germination on filter paper

7.2.1.1 Methods

Glass petri dishes (9 cm diameter) containing two moistened filter papers (Whatman No.1, 9 cm) were used for germination tests. Twenty-five fully-developed E. incrassata seeds obtained from mature capsules were placed in each petri dish. The petri dishes were kept at constant temperature (20°C) under twelve-hourly, alternating periods of light and dark.

Germinating seeds were counted and removed daily. Seeds were regarded as having germinated when the cotyledons were emerging from the seed coat (Scott 1972). The tests were terminated when fourteen days had elapsed without any further germination. Ungerminated seeds were

examined for signs of abnormality. In almost all cases, attack by fungal pathogens had resulted in necrosis of the embryo. These seeds were classified as non-viable. The number of germinated seeds was expressed as a percentage of the total seeds to provide an estimate of seed viability. As in previous chapters, sample variability is expressed as the standard deviation about the mean, unless otherwise stated.

7.2.1.2 Results and discussion

Ten replicates of twenty-five seeds were tested as described above. The mean number of germinants obtained per twenty-five seeds was 20.7 $\pm$ 1.6, which represents a viability of 82.8 $\pm$ 4.6% for fully-developed seeds.

It is not known whether all seeds were viable when selected. Examination of the embryos of a further fifty fully-developed seeds indicated forty-nine "firm white embryos"; seeds in this condition were classified as viable by Grose and Zimmer (1957). Holland (1967) conducted germination tests on seeds of E. incrassata and demonstrated >90% viability. It is possible that some non-viable seeds were included in the samples used. Pathogen attack on viable seeds following water imbibition may also have contributed to the lower germination rate observed in the present study compared to the germination rates measured by Holland (1967).

The seeds of some Eucalyptus species have been demonstrated to be dormant under particular conditions (Boden 1957). However, tests conducted by Larsen (1965) and Scott (1972) indicate that E. incrassata seeds are non-dormant. The high germination rates obtained in the present study together with the lack of viability amongst non-germinated seed support this conclusion.

7.2.2 Laboratory germination in soil

7.2.2.1 Methods

Surface soil samples were collected from unburnt mallee communities close to the field sites. The samples were sieved with a 1.0mm sieve to remove any resident seeds of *E. incrassata*. Two hundred fully-developed *E. incrassata* seeds were added to each sample. The samples containing seed were spread to a depth of 2cm in plastic germination trays (28 x 33 x 5 cm); they were then placed in a glasshouse (ca 20°C) and irrigated daily with tap water.

Emerging seedlings were counted and removed daily. The experiment was discontinued when no further germination had occurred over a period of six weeks.

7.2.2.2 Results and discussion

The mean number of germinants obtained for nine replicates of two hundred seeds sown in soil was 94.0 ± 15.8, which represents a mean percentage germination of $47.0 \pm 7.9\%$. This figure is considerably lower than the percentage germination obtained using moist filter paper as a substrate (Section 7.2.1.2). Cremer (1965c) also obtained low germination rates (up to 51%) for *E. regnans* seeds sown in soil.

The reasons for the dramatic reduction in percentage germination of seeds sown in soil, when compared to germination of similar seeds placed on filter paper, remain unclear. The technique used to monitor the germination of seeds in soil requires each newly-germinated seedling to break the soil surface. The measurements were actually of 'emergent' seedlings rather than of 'germinants'. It is possible that a certain proportion of seeds actually germinate in soil, but are unable to reach the surface either as a result of depth of burial (Free 1951), or as a

consequence of pathogen attack soon after germination (Cremer 1965c). Another possible factor contributing to reduced germination in soil is the low oxygen and high carbon dioxide content of the soil environment; both of these factors are known to inhibit seed germination of many plant species (Cremer 1965c).

7.3 Factors influencing germination

7.3.1 The effects of sowing depth on seedling emergence

7.3.1.1 Introduction

One factor which may contribute to the lower rates of seedling germination and emergence from a soil substrate compared to a moist filter paper substrate (Section 7.2.2) is the effect of sowing depth on seedling emergence. To investigate this effect, an experiment was set up in which seeds were sown in soil at various depths down to 2.0cm.

7.3.1.2 Methods

Soil was added to five standard germination trays, to depths of 2.0cm, 1.9cm, 1.5cm, 1.0cm and <0.1cm. One hundred seeds were scattered evenly across the soil surface of each tray. More soil was then added, resulting in a final soil depth of 2.0cm in each tray; the five samples thus represented sowing depths of 0cm, 0.1cm, 0.5cm, 1.0cm and 2.0cm. Another soil sample of similar volume, to which one hundred seeds had been added, was mixed thoroughly by shaking in a plastic bag, and was then added to a sixth germination tray. The six trays were placed in a glasshouse, irrigated daily and monitored as described above.

Comparisons were made between the number of emergent seedlings in each sample and the mean number of emergents over all samples on the fourth, tenth, fifteenth, twentieth and twenty-fifth day after first seedling emergence.

The chi-square test (Sokal and Rohlf, 1969; chapter 16, pp550-600) was used for the majority of the statistical comparisons described in this chapter. Where other tests were used, specific references are given in the text.

7.3.1.3 Results and discussion

Germination results for the six depth treatments are presented in Table 7.1.

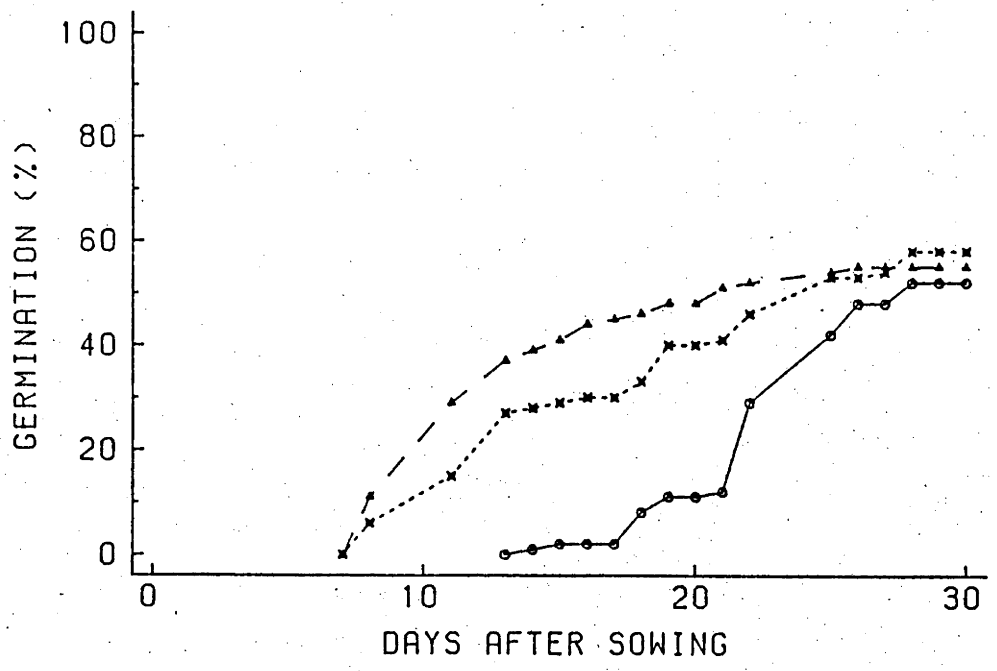
Table 7.1 Germination results for E. incrassata seeds sown in soil at six depths (n = 100 seeds).

Sowing depth (cm)	Total % germination	Time to start germination (days)
surface	60	14
.1	61	8
.5	56	8
1.0	60	9
2.0	47	13
mixed	53	11

Comparisons between the total number of germinants from different depths indicated significantly fewer germinants from seeds sown at 2.0cm than from seeds sown at 0.1cm depth ($X^2_{(1)} = 3.945$, $P<.05$*). Comparisons amongst all other treatments indicated no significant differences in total germination (eg. 2.0cm vs 1.0cm, $X^2_{(1)} = 3.397$, $P>.05$). The reduced number of germinants evident in the samples sown at 2.0cm and mixed through the profile compared to sowing depths other than 0.1cm therefore indicates a small, statistically insignificant effect on emergence due to sowing depths below 1.0cm.

Emergence rates of seedlings from seeds sown at five depths (see above) and from seeds mixed through the profile, are plotted in Figure 7.1. Comparisons between the number of emergent seedlings for each sample and the mean number of emergents from all samples were carried out at approximately five day intervals. The results indicate that sowing depth to 2.0cm affects early rates of emergence, but has little effect on the number of emergent seedlings between ten and twenty-five days after first emergence (Table 7.2).

It is evident from a consideration of Figure 7.1 that seeds sown at depths between 0.1cm and 1.0cm exhibited early and rapid germination whereas seeds sown either at 2.0cm depth or on the soil surface exhibited late and slow germination. Samples sown at 0.1cm, and 1.0cm depth also exhibited high percentage germination (Table 7.1). Sowing depths between 0.1cm and 1.0cm were therefore optimal for seeds of E. incrassata in this experiment. Reasons for the decrease in total percentage germination in the sample sown at 0.5cm are not clear, but it is likely that variability of both soil samples and seed samples, and heterogeneity of soil environments may have contributed to this result.



The effects of sowing depth on germination of seeds of E. incrassata, (n = 100 seeds)

Depth: surface - solid line
0.1cm - dotted line
0.5cm - dashed line

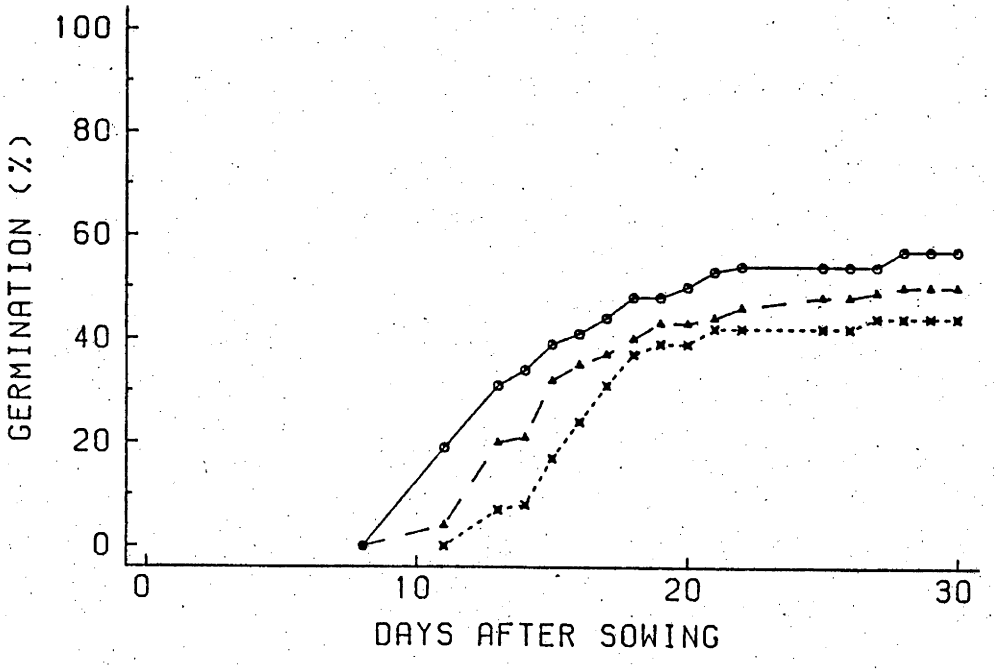


Figure 7.1 The effects of sowing depth on germination of seeds of E. incrassata (n = 100 seeds)

Depth: 1.0cm - solid line
2.0cm - dotted line
mixed - dashed line

Table 7.2 The effects of sowing depth (to 2.0cm) on seedling emergence (n = 6 depths)

No. of days after first emergence	Mean no. of germinants (n=100seeds)	$X^2_{(5)}$	P
4	11.17	62.20	<.001***
10	31.50	39.42	<.001***
15	44.83	8.86	>.1
20	50.67	1.89	>.5
25	55.00	3.41	>.5

Free (1951) investigated the effects of sowing depth on germination and emergence of the seed of several species of Eucalyptus. He demonstrated a correlation between seed size and depth of sowing from which emergence could take place. Scattered large seeds emerged from depths down to 1.25cm, but scattered small seeds emerged only from depths to 0.75cm. Seed of some species could emerge from depths down to 3.8cm when sown in heaps. The optimal depth for germination and emergence for all species investigated in Free's (1951) study was between 0.5cm and 0.75cm. Another detailed investigation of the emergence of E. regnans seedlings from buried seed indicated an optimal sowing depth of 0.6cm (Cremer 1965c). These values are similar to the optimal sowing depths for E. incrassata demonstrated in the present study.

In the investigations by Cremer (1965c) referred to above, surface-sown seed exhibited slow rates of germination, and the final germination percentages were significantly lower than the percentages for deeper-sown seed. Free (1951) speculated that poor germination of shallow-sown seed may be due to a sensitivity of some species to desiccation during germination, the chances of desiccation being greater in the surface layers. This phenomenon has been demonstrated for several plant species (Miller and Perry 1968, Mott 1974).

Results obtained in the present study indicate similar slow initial germination rates for surface-sown seed (Figure 7.1). However, the germination rates of shallow-sown (0.1cm) seed were high (Figure 7.1), and the final numbers of germinants were similar for most samples (Table 7.2). Desiccation may have contributed to the slow germination rates of surface-sown seeds, but apparently did not influence final germination percentages in the present investigation.

The sample with seed mixed through the profile exhibited a similar overall germination response to samples with seed sown at depths between 0.1cm and 2.0cm (Figure 7.1). This result indicates that the germination technique described in Section 7.2.2 is unlikely to have influenced the final germination percentages obtained for seeds in a soil substrate. The final germination percentages described in the present section (mean % germination = $56.2 \pm 5.4\%$) confirm that germination of seed in soil is significantly less than germination of seed on a moist filter paper substrate.

7.3.2 The effects of light and temperature on seed germination on filter paper

7.3.2.1 Introduction

The seed of most eucalypt species has an optimum temperature for germination. E. incrassata seeds have been shown to exhibit optimal germination at a constant temperature of 20°C (Scott 1972).

The effects of light on the germination of Eucalyptus seed are variable. Some species require light for germination, others do not, and for some species, continuous light inhibits germination (Grose and Zimmer 1957). Clifford (1953) noted that mature seeds of E. incrassata do not require light for satisfactory germination; his germination tests were carried out at a constant temperature of 24°C.

For some eucalypt species, temperature and light appear to interact in their effects on germination (Grose and Zimmer 1957). A detailed study of the germination responses of E. camaldulensis seeds indicated that light is required for germination of this species. However the light requirements of E. camaldulensis vary with temperature; they are least at temperatures close to the optimum germination temperature, and increase with temperature above or below this (Grose and Zimmer 1958).

This section describes investigations of the germination response of E. incrassata seeds to different temperature and light regimes. The investigations include:-

1. an examination of the effect of three constant temperatures (viz: 10°C, 20°C, 30°C), and two light regimes (viz: twelve hours light and continuous darkness) on germination behaviour

2. an examination of the effect of two alternating temperature regimes (viz: 20°/10°C and 30°/20°C) and two light regimes (as above) on germination behaviour.

7.3.2.2 Methods

Glass petri dishes, each containing twenty-five fully-developed E. incrassata seeds were set up according to the method described in Section 7.2.1.1. Controlled-environment cabinets were used to provide a twelve-hour light period and the required temperature regimes. Conditions of continuous darkness were achieved by enclosing the petri dishes in aluminium foil.

Eight replicates of twenty-five seeds were set up under constant temperature regimes of 10°C, 20°C and 30°C. Each temperature regime included four replicates with a twelve hour light period and four replicates in continuous darkness. A further four replicates were placed in a refrigerator at a constant temperature of 5°C and under conditions of continuous darkness. Practical reasons prevented any treatments with a twelve hour light period being set up at this temperature.

Seeds were also placed under alternating temperature regimes of 20°/10°C and 30°/20°C. Two replicates of twenty-five seeds were placed in a twelve hour light regime, and a further two replicates under conditions of continuous darkness, in each temperature regime.

Germination of seeds under the different conditions was monitored according to the methods described in Section 7.2.1.1.

7.3.2.3 Results and discussion

Constant temperatures of 20°C and below had no significant effect on the total percentage germination of E. incrassata seeds irrespective of photoperiod (Table 7.3a).

Constant temperatures of 30°C significantly inhibited germination both under a twelve hour photoperiod (30°C vs 20°C, $X^2_{(1)} = 97.059$, P<.001***), and under conditions of continuous darkness (30°C vs 20°C, $X^2_{(1)} = 108.953$, P<.001***). E. incrassata seeds apparently experience an induced dormancy as a result of high temperatures. Rates of increase in percentage germination under the different conditions of light and temperature are plotted in Figure 7.2. Optimal germination in terms of both rate and total number of germinants occurred at 20°C. Lower temperatures increased the time taken for germination to commence after sowing, but did not influence the final number of germinants (Table 7.3a, Figure 7.2). The treatment at 5°C exhibited slower rates of germination. High temperatures (30°C) did not influence the time taken for germination to commence, but reduced the rate of germination as well as the number of seeds which had germinated by thirty days after sowing (Figure 7.2).

A more realistic approximation of field temperatures was attempted using alternating temperature regimes. A 'summer' regime (30°/20°C) and a cooler 'spring-autumn' temperature regime (20°/10°C) were used (see Table 7.3b).

Germination responses to the two alternating temperature regimes under both light and dark conditions are plotted in Figure 7.3. Comparisons of the effects of the alternating temperature and light treatments are included in Table 7.4.

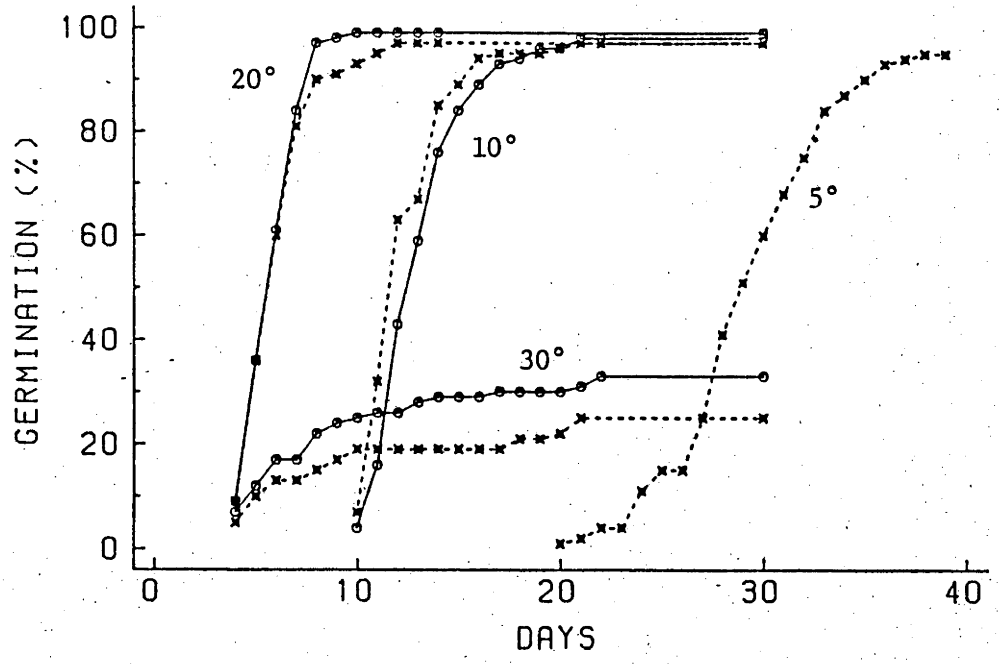


Figure 7.2 The effects of constant temperature and a twelve-hour photoperiod on germination of E. incrassata seeds (n = 100seeds)

continuous dark - dotted lines
twelve-hour light - solid lines

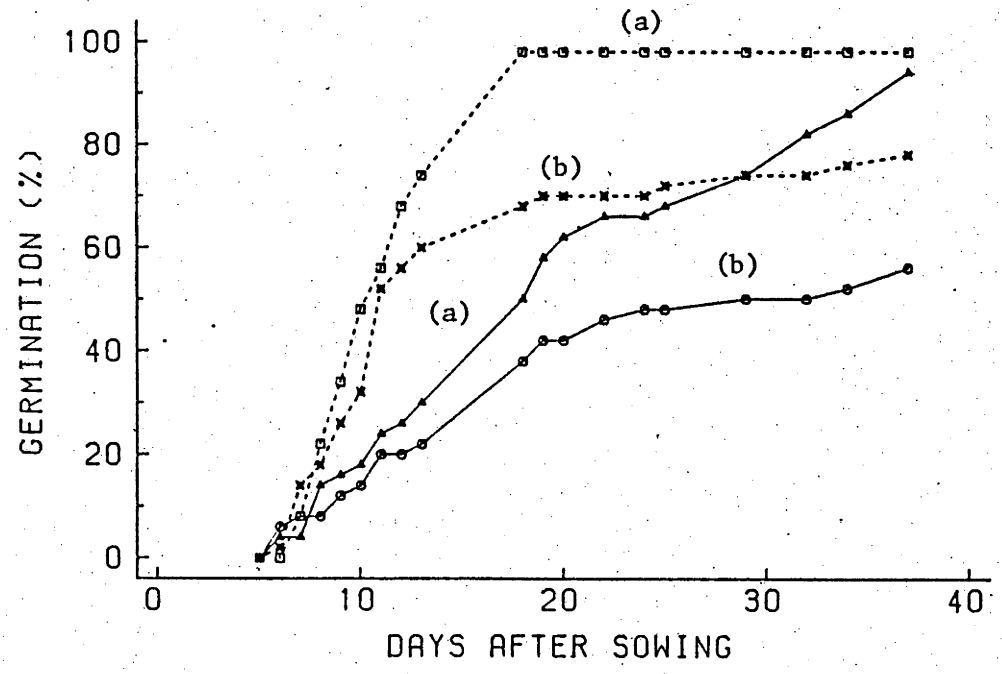


Figure 7.3 The effects of alternating temperature and a twelve-hour photoperiod on germination of E. incrassata seeds (n = 50 seeds)

(light conditions - as above)
a = 20°/10°C ; b = 30°/20°C

Table 7.3 Germination results for *E. incrassata* seeds under different temperature and light regimes (filter paper substrate)

Treatment	Total % germination	Time to start germination (days)
a. Constant temperature (n=100)		
5°C dark	95	20
10°C light	98	10
10°C dark	97	10
20°C light	99	4
20°C dark	97	4
30°C light	33	4
30°C dark	25	4
b. Alternating temperature (n=50)		
20°/10°C light	94	5
20°/10°C dark	98	6
30°/20°C light	56	5
30°/20°C dark	78	5

Table 7.4 The effects of alternating temperatures and a twelve hour light period on the germination of E. incrassata seeds (n = 50 seeds) (filter paper substrate)

Comparison	Condition	$X^2_{(1)}$	P
12 hours light v dark	30°/20°C	5.473	<.05*
12 hours light v dark	20°/10°C	1.042	>.1
30°/20°C v 20°/10°C	12 hours light	24.901	<.001***
30°/20°C v 20°/10°C	continuous dark	9.470	<.005**

Light had no significant effect on the total percentage germination of E. incrassata seeds under a 20°/10°C alternating temperature regime. However, under a 30°/20°C temperature regime, exposure of seeds to a twelve hour light period caused a significant reduction (22%) in total percentage germination (Table 7.4). High temperatures significantly reduced the total number of germinants irrespective of whether the seeds were in continuous darkness or were exposed to a twelve hour light period (Tables 7.3 and 7.4).

The reasons why a twelve-hour photoperiod significantly reduced germination under an alternating temperature regime of 30°/20°C (Table 7.4), yet produced a slight but statistically insignificant increase in germination at a constant temperature of 30°C ($X^2_{(1)} = 1.554$, P>.1) are not clear. It is possible that sample variability caused the increased germination at constant temperature (30°C), and that light effects evident under alternating temperatures were overridden by a constant high temperature.

The alternating temperature data indicate that seed germination in the field would be significantly reduced (>20% reduction) during the warmer months of the year. The combined effects of a twelve hour light period and a 30°/20°C temperature regime resulted in a 38% reduction in total seed germination in the present experiment (Figure 7.3).

Monthly mean maximum temperatures at the field sites exceed 30°C during December, January and February, and exceed 25°C over the period from November to March (Table 3.1; Figure 3.4). The effects of high temperatures and exposure to at least twelve hours of light in summer would effectively inhibit most germination of surface seed, even if soil moisture levels were high. The high evaporation rates which occur in summer (Section 3.2.1.2) result in rapid drying of the upper layers of the soil following rain. Low soil moisture levels and high temperature inhibition effectively confine germination to the cooler months of the year. Soil moisture levels are also high during autumn, winter and early spring (Figures 3.5a and 3.5b); these seasons are thus the most favourable for germination. Light inhibition of germination at high temperatures further enhances this effect.

7.3.3 The effects of heat-treated soil on germination of *E. incrassata* seed under two alternating temperature regimes.

7.3.3.1 Introduction

Increased germination of a wide range of plant species, including eucalypts, has been commonly recorded in recently-burnt areas (Beadle 1940, Cremer and Mount 1966, Floyd 1976, Purdie 1976, 1977). Soil temperatures measured during fires indicate that surface temperatures may exceed 200°C, but temperatures exceeding 100°C rarely occur below

5cm depth (Beadle 1940). Heat treatment of soil has been shown to have a stimulatory effect on the germination of seeds resident in the soil prior to heating (Warcup 1980).

E. incrassata seed is seldom present in soil in long-unburnt stands, but is apparently released onto the soil surface in large quantities following fire (see Chapter 6). It is likely that most of the seed released after a fire does not experience high temperatures during the fire since it is enclosed in thick-walled, woody fruits. If this is the case, then the high germination rates of E. incrassata observed following fire (Chapter 4) may be influenced by changes to the soil caused by the fire.

The present section describes an experiment investigating the effects of heat treatment of soil on the germination of seeds added to the soil after heating.

7.3.3.2 Methods

Soil samples collected from the field sites were sieved with a 1.0mm sieve, heated in an electric oven to 180°C and maintained at this temperature for half an hour. Heating soil to temperatures greater than 180 C has been shown to produce a stimulatory effect on Eucalyptus growth similar to the 'ash-bed' effect observed in the field following fire (Pryor 1960).

Heated and control soil samples were spread to a depth of 1.5cm in plastic germination trays (28 x 33 x 5 cm). Fifty fully-developed E. incrassata seeds were scattered across the surface of each soil sample, and were subsequently covered with a further layer of soil to a depth of 0.5cm; sowing at depths of between 0.1cm and 1.0cm results in optimal germination rates for E. incrassata seeds (Section 7.3.1).

Controlled environment cabinets were used to provide two alternating temperature regimes (viz: 30°/20°C and 20°/10°C) and a twelve-hour photoperiod to simulate summer and spring/autumn field conditions. Two replicates of both heated and unheated soil were placed in each environment. The soil was kept moist by daily irrigation with distilled water. Germination was monitored as described in Section 7.2.2.1.

7.3.3.3 Results and discussion

The germination data for seeds sown in heat-treated and control soil samples are summarized in Table 7.5.

Table 7.5 Germination results for E. incrassata seeds sown in 'heated' and 'control' soil samples under two alternating temperature conditions (n = 100 seeds).

Treatment	Total % germination	Time to start germination (days)
20°/10°C heated	88	8
20°/10°C control	61	10
30°/20°C heated	70	6
30°/20°C control	38	8

Heat treatment of soil decreased the time between sowing and first emergence and increased the total number of emergents. Germination rates of seeds in heated and unheated soil at the two temperature regimes are plotted in Figure 7.4. Comparisons of the total number of germinants in each treatment are included in Table 7.6.

Table 7.6 The effects of heated soil on germination of *E. incrassata* seeds under two alternating temperature regimes (n = 100 seeds)

Comparison	Condition	$X^2_{(1)}$	P
Heated v Control	30°C/20°C	20.612	<.001***
Heated v Control	20°C/10°C	17.568	<.001***
30°/20°C v 20°/10°C	Heated soil	8.562	<.005**
30°/20°C v 20°/10°C	Control	10.687	<.005**

Heating soil at 180°C for half an hour significantly increased the total germination of seeds added to the soil after heating, irrespective of the subsequent air temperature regime (Table 7.6). The total number of seeds germinating under a 30°/20°C temperature regime in both heated and unheated soil samples was significantly less than germination in similar samples at 20°/10°C. Heated soil also increased the rate of germination of *E. incrassata* seeds, particularly under a 30°/20°C temperature regime (Figure 7.4). Germination was more rapid in heated samples than in the controls during the fifteen days following first emergence.

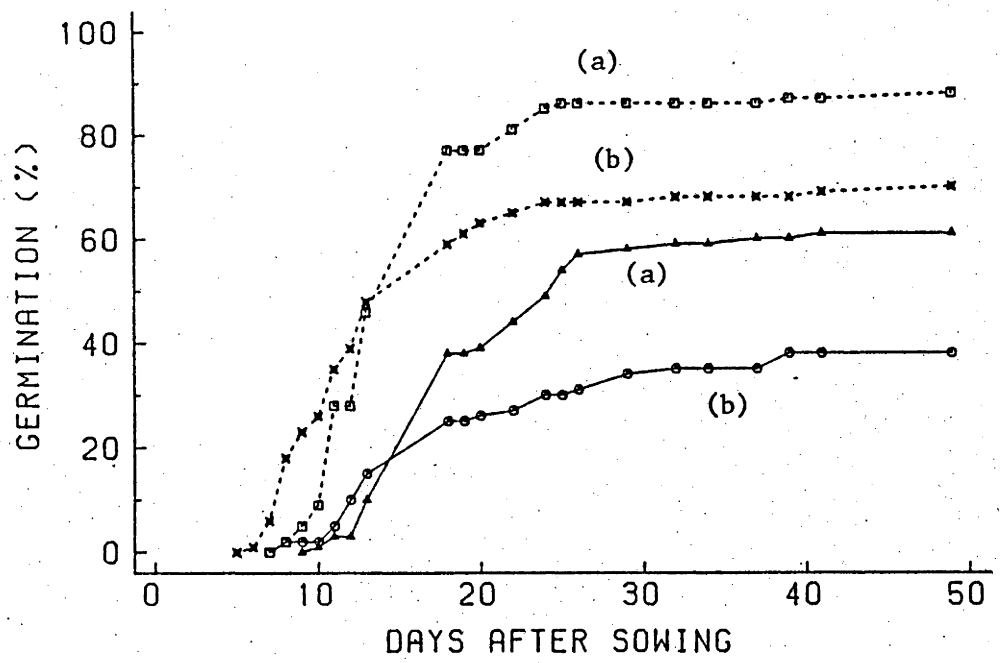


Figure 7.4 The effects of heat treatment of soil on germination of E. incrassata seeds under two alternating temperature regimes (viz: a = 20°/10°C ; b = 30°/20°C)

heated soil - dotted lines
control soil - solid lines

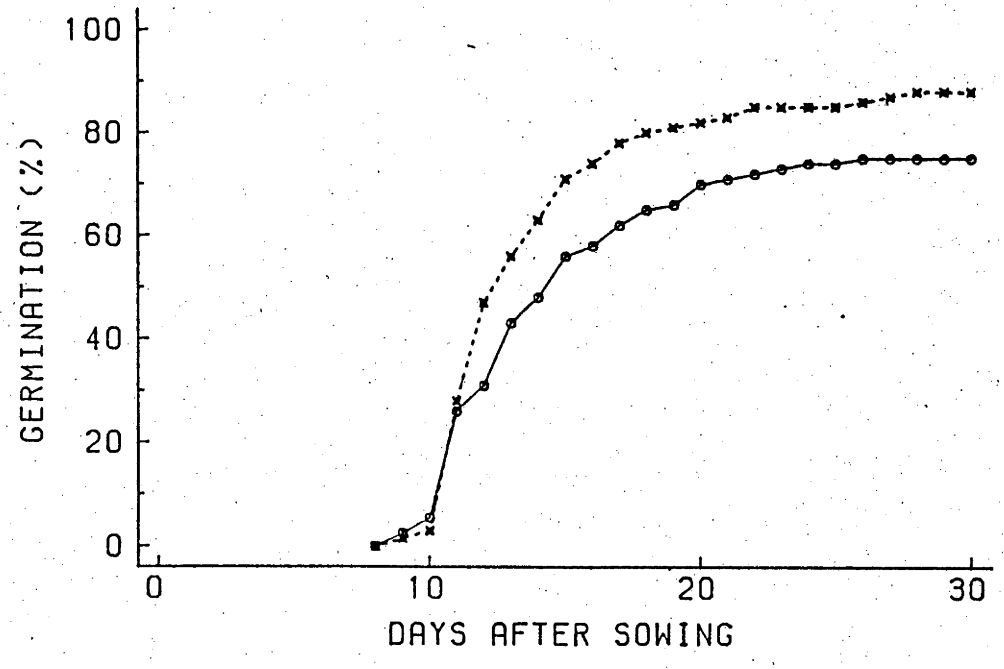


Figure 7.6 The effect of naturally - burnt soil on germination of E. incrassata seeds under laboratory conditions (n = 200 seeds)

burnt soil - dotted line
control - solid line

These data indicate that soil heating is likely to be an important component of an 'ash-bed' effect (Pryor 1960) on germination. The results also confirm that high temperatures inhibit the germination response of E. incrassata seeds in soil as well as on a filter paper substrate (Section 7.3.2).

7.3.4 The effects of 'fire factors' on germination of E. incrassata seeds

7.3.4.1 Introduction

E. incrassata seeds exhibit higher germination rates and an increase in total percentage germination when sown in heat-treated soil (Section 7.3.3). Factors other than soil-heating may contribute to the enhanced germination effect observed following fire. An experiment designed to investigate the separate and combined effects of ash addition, litter removal and heat treatment of soil is described in the following sections.

7.3.4.2 Methods

Soil samples were prepared as described in Section 7.3.3.2. Heated and unheated samples were placed in 15cm diameter plastic pots. In each pot, twenty-five fully-developed E. incrassata seeds were added to the soil surface at 3cm intervals, forming a 12 x 12 cm grid. The seeds were covered with a further 0.5cm of soil. Another layer (0.5cm depth) of either sand, ash, litter or a 50% ash + 50% litter mixture was then added to the soil surface, resulting in eight treatments (viz: control, +ash, +litter, +heat, +ash+litter, +ash+heat, +litter+heat, +ash+litter+heat). Four replicates of twenty-five seeds were included in each treatment.

The pots were placed in a glasshouse (approximately 20° ± 5° C) and irrigated daily with distilled water. Newly-emergent seedlings were recorded daily. The experiment was discontinued when no further germination had occurred over a period of six weeks.

Final germination percentages were transformed using the angular transformation (Sokal and Rohlf 1969, pp 386-387) and tested for homoscedasticity (F max-test; Sokal and Rohlf 1969, p 371). A three-way analysis of variance and the t-test were used to test the significance (0.05%) of germination differences.

7.3.4.3 Results and discussion

Germination results of seeds sown under different 'fire factor' treatments are included in Table 7.7.

To investigate the effects of the different 'fire factors' treatments on germination, a three-way analysis of variance was conducted on transformed final percentage germination data (Table 7.8).

The results of the analysis of variance indicated that both the heat-treated soil and the addition of ash to the soil surface caused a significant increase in the number of germinants (Table 7.8). The presence of litter on the soil surface had no significant effect on seed germination. There was no evidence of any significant interaction effects between the different treatments.

The germination responses to the eight 'fire factor' treatments are plotted in Figure 7.5. Seeds sown in heat-treated soil exhibited consistently higher germination rates than seeds sown in unheated soil, which supports the results described in Section 7.3.3.3. The heat treatment and the addition of ash also caused a slight reduction in the

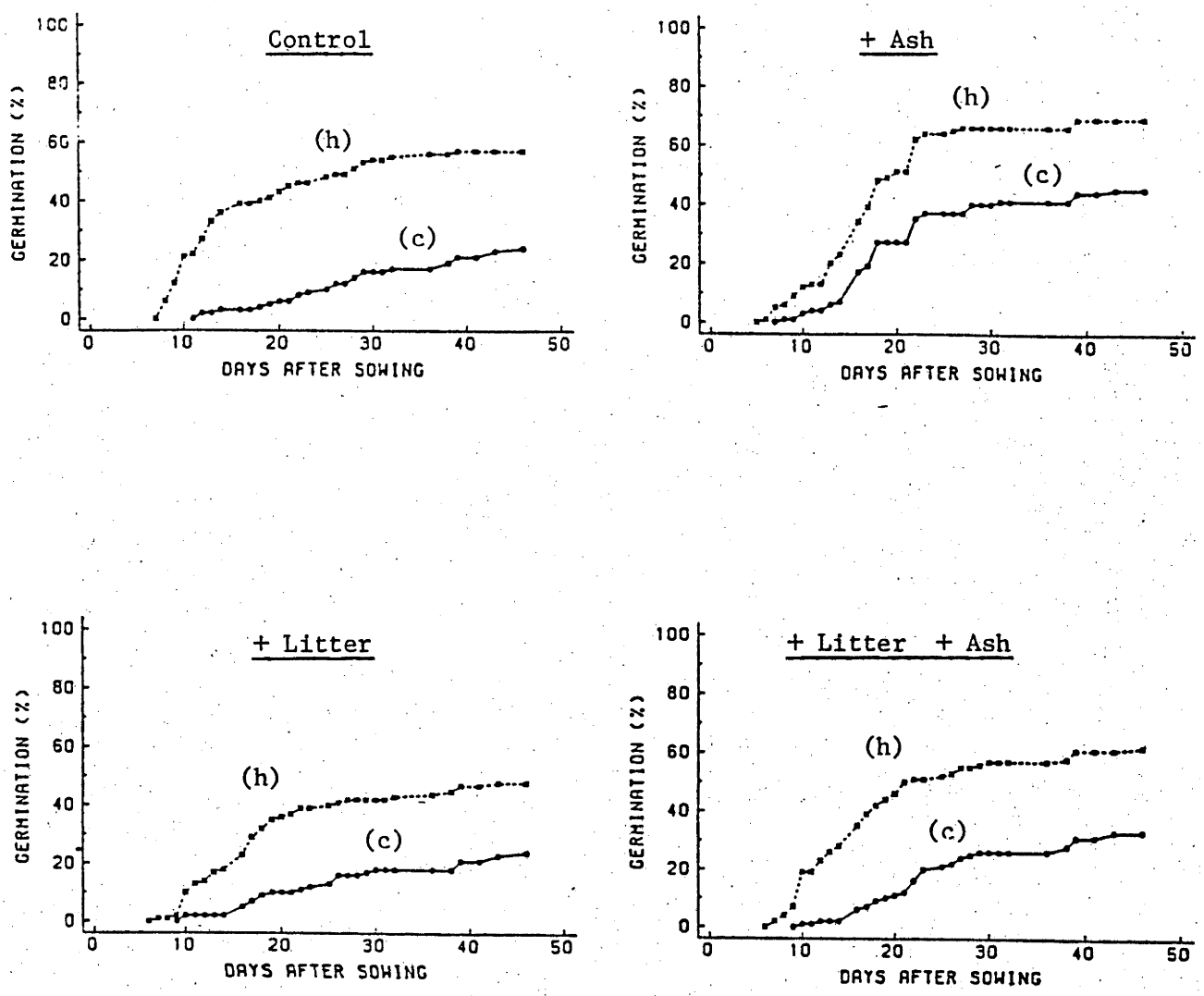


Figure 7.5 The effects of 'fire factors' on the germination of E. incrassata seeds sown in soil (n = 100 seeds)
(c) = unheated soil
(h) = heated soil

Table 7.7 Germination results for *E. incrassata* seeds sown in soil subjected to 'fire factor' treatments (n = 100 seeds)

Treatment	Total % germination	Time to start germination (days)
control	26	11
+ litter	28	9
+ ash	63	7
+ heat	58	7
+ ash + litter	46	9
+ heat + litter	49	6
+ heat + ash	70	5
+ heat + ash + litter	66	6

Table 7.8 Three-way analysis of variance on transformed percentage germination data for the 'fire factors' experiment (from Table 7.7)

Source of variation	df	F	P
Main effects:			
Heat	1	18.910	<.001***
Ash	1	17.160	<.001***
Litter	1	1.380	.252
2-way interactions:			
Heat x Ash	1	1.795	.193
Heat x Litter	1	.034	.854
Ash x Litter	1	.860	.363
3-way interactions:			
Heat x Ash x Litter	1	1.020	.323

time between sowing and first emergence (Table 7.7).

Germination of E. incrassata in an ashbed following a fire is apparently enhanced both by the presence of ash and by heating of the soil caused by the fire. The effects of these factors are additive, and the combined effect is significantly greater than either ash addition ($t_{(6)} = 2.876$, $P<.05$*) or heat treatment alone ($t_{(6)} = 2.491$, $P<.05$*). The presence of litter in samples with ash added to heat-treated soil, did not significantly alter total percentage germination ($t_{(6)} = 0.432$, $P>.5$) although a slight reduction in germination did occur (Figure 7.5).

The exact nature of changes to a soil substrate caused by a fire are unknown. Increases in soil nutrient levels resulting either from nutrient release from ash or from the breakdown of microbial thalli (Pryor 1960) almost certainly contribute to the enhanced growth rates of seedlings. Increased soil nutrient status may also influence seed germination. In the present study, both the heated-soil treatment and the ash-addition treatment may have altered the soil nutrient levels; however, this was not tested.

Fire-associated changes to a soil are known to have a profound effect on microbial populations in the soil. Sterilization due to heating of the soil occurs in intense fires, and results in a prolonged process of recolonization and subsequent succession before the microflora reverts to a 'pre-burn' composition (Renbuss et al. 1972). Suppression of species detrimental to germination and seedling growth, or the promotion of beneficial species may contribute to the observed 'ashbed' effect. Further studies would be necessary to determine whether any or all of these factors are important in the observed germination responses of E. incrassata to fire-associated changes in the soil.

The data presented in this section indicate that fire is likely to play an important role in sexual regeneration of E. incrassata by significantly enhancing the germination response of seeds in soil. Specific factors which influence germination are heat treatment of the soil (180°C) and the addition of ash. The presence of litter does not appear to influence germination of buried seed.

7.3.5 Germination of E. incrassata seeds in recently-burnt soils

7.3.5.1 Introduction

Results described in the previous section indicate that factors associated with the effects of fire on mallee soils cause a significant increase in the germination response of E. incrassata seeds. The occurrence of a fire on 18 January 1981 in an area close to the study sites provided an opportunity to verify these results. The present section describes an experiment in which seed was added to both recently-burnt and long unburnt mallee soils and the germination responses were compared.

7.3.5.2 Methods

Surface soil from an area burnt on 18 January 1981 and an adjacent long-unburnt area, both located close to the study sites, were collected on 30 January 1981. Fully-developed E. incrassata seeds were sown in sample of these two soils as described in Section 7.3.3.2. Four replicates of fifty seeds were sown in samples of each soil type. The samples were maintained under a twelve-hourly alternating temperature regime of 20°/10°C and a twelve-hour photoperiod. The soil was kept moist by daily irrigation with distilled water. Germination was monitored as described in Section 7.2.2.1.

7.3.5.3 Results and discussion

The germination results obtained for seeds added to recently-burnt and long-unburnt soils are presented in Table 7.9 and Figure 7.6.

Table 7.9 Germination results for E. incrassata seeds sown in recently-burnt and long-unburnt soils (n = 200 seeds)

Soil type	Total % germination	Time to start germination (days)
Burnt 1981	88	9
Long-unburnt	75	9

The total number of germinants from the recently-burnt soil samples was significantly greater than from long-unburnt soils ($X^2_{(1)} = 10.256$, $P<.005$**). This result further supports the hypothesis that fire-induced changes to the soil enhance germination (see Section 7.3.4).

The difference between germination responses in burnt soil and unburnt soil (Figure 7.6) is not as great as might be expected in view of the results obtained from the 'fire factors' experiment (Section 7.3.4.3). However, germination responses in both treatments were elevated in relation to the 'fire factors' results. Conditions associated with particular germination environments in the present experiment may have contributed to the enhanced results in both soil types. A comparison of the results in Section 7.3.3.3 with those in Section 7.3.4.3 indicate that part of the enhancement effect may be due

to the use of a growth cabinet rather than a glasshouse as a germination environment. The results in Section 7.3.3.3 which were obtained using a growth cabinet and a temperature regime of 20°/10°C were similar to those obtained in the present section under similar conditions. It is possible that temperature fluctuations in the glasshouse environment decrease germination. It is also possible that variability between soil samples collected from different sites and at different times is high owing to microflora and nutrient differences (see Section 7.2.2), and thus contributes to the variability in germination evident between similar treatments in different experiments.

Actual soil temperatures measured during natural fires are high at the soil surface, but decrease rapidly with depth (see Beadle 1940). Litter in unburnt stands is also very 'patchy'. It is likely that changes to the soil during a fire as a result of heating and ash addition are highly variable, and that fires result in very complex horizontal and vertical gradients of change to the soil. It is probable that a mosaic of favourable sites and unfavourable sites for germination occurs in the soil after fire, and that these sites have a strong influence on recruitment.

7.3.6 The effects of storage on seed viability

7.3.6.1 Introduction

Mature eucalypt seed remains viable for periods of between five and twenty years when stored under dry conditions at a temperature between 3°C and 5°C (Boland *et al.* 1980). The seeds of many species also retain a high viability when stored dry under ambient conditions (Grose and Zimmer 1958). The moisture content of seed is a critical factor influencing storage life: low moisture contents (<8%) and an ambient

relative humidity of <40% result in greater longevity (Suiter and Lisbao 1973).

Ewart (1908) examined 200 seeds of E. incrassata which had been stored under dry conditions for fifty-seven years; none of these were viable. Of the thirty-six eucalypt species examined by Ewart (1908), the seeds of most species were found to retain some viability for up to twenty years storage time, and the seeds of a few species were viable for periods of up to thirty-seven years. Ewart (1908) also noted that in general, seed longevity is less when seeds are stored in soil than when they are stored in air in a dried condition.

Under natural conditions, the seed of many eucalypt species including E. incrassata is stored in capsules in the canopy for periods of up to three or four years (Section 6.3). There is apparently no long-term storage of seed in the soil, although seed is present on the soil surface at certain times of the year (Section 6.5).

In the present study, seed was collected annually over a period of two years and stored in a dry state under laboratory conditions. Additionally, an experiment was set up in which seed was buried in soil in an unburnt stand of E. incrassata. This section describes investigations into the effects of storage under these conditions on the viability of E. incrassata seed.

7.3.6.2 Methods

Mature capsules of E. incrassata were collected from an unburnt area adjacent to the field sites in December 1978, December 1979 and August 1980. Capsules were collected from a large number of trees (n>30). The capsules were air-dried and the seed and chaff were removed and separated with a 1.0mm sieve. The coarse fraction, which included

seeds and aggregates of chaff, was then stored in manilla envelopes under laboratory conditions (approximately 20°C and 40% relative humidity).

Between December 1979 and January 1980, a heavy flowering season occurred for E. incrassata in the area adjacent to Lake Albacutya (see Section 6.2). A large crop of seed capsules developed following the flowering season. By August 1980, the new capsules were still ripening and were green in colour. At the same time as the mature capsules were collected in August 1980, a sample of the new, ripening capsules was also collected. Seed was obtained from these and stored in the manner described above.

Fully-developed seeds were selected from the four seed collections in November 1980. Four replicates of twenty-five seeds from each seed collection were placed on filter paper in glass petri dishes and maintained under conditions similar to those described in Section 7.2.1.1. Germination was monitored according to the methods described in Section 7.2.1.1. The chi-square test was used for comparisons of germination responses for seeds of different storage age.

An experiment was described in Section 6.6.5 in which E. incrassata seeds collected in December 1979, were buried in soil in an unburnt mallee stand in February 1980. The results from that experiment (Section 6.6.5.2, Table 6.11) are used in the present section in order to compare the longevity of seeds stored in soil under field conditions for differing periods of time, with seeds which had never been stored in soil (Section 7.2.2.2).

7.3.6.3 Results and discussion

Total percentage germination results for seeds of different storage age are included in Table 7.10.

Table 7.10 Germination results for *E. incrassata* seeds stored under laboratory conditions for different periods (filter paper substrate) (n = 100 seeds)

Vintage	Storage time (years)	Total % germination	Time to start germination (days)
Pre-1980	2	93	5
Pre-1980	1	95	4
Pre-1980	0.3	88	5
1980	0.3	95	5

Comparisons between the total number of germinants obtained for each storage age indicated that storage time had no significant effect on seed viability (e.g. pre-1980 (1yr) vs pre-1980 (0.3yr), $X^2_{(1)} = 3.150$, $P>.05$). Similarly, there was no significant difference in the total number of germinants between seeds from mature (pre-1980) capsules and seeds from green (1980 vintage) capsules. The germination responses for seeds of different storage ages and vintages are plotted in Figure 7.7.

It is apparent from the curves in Figure 7.7 that large differences occurred in the daily total number of germinants between treatments over the period from the fifth to the fourteenth day following sowing.

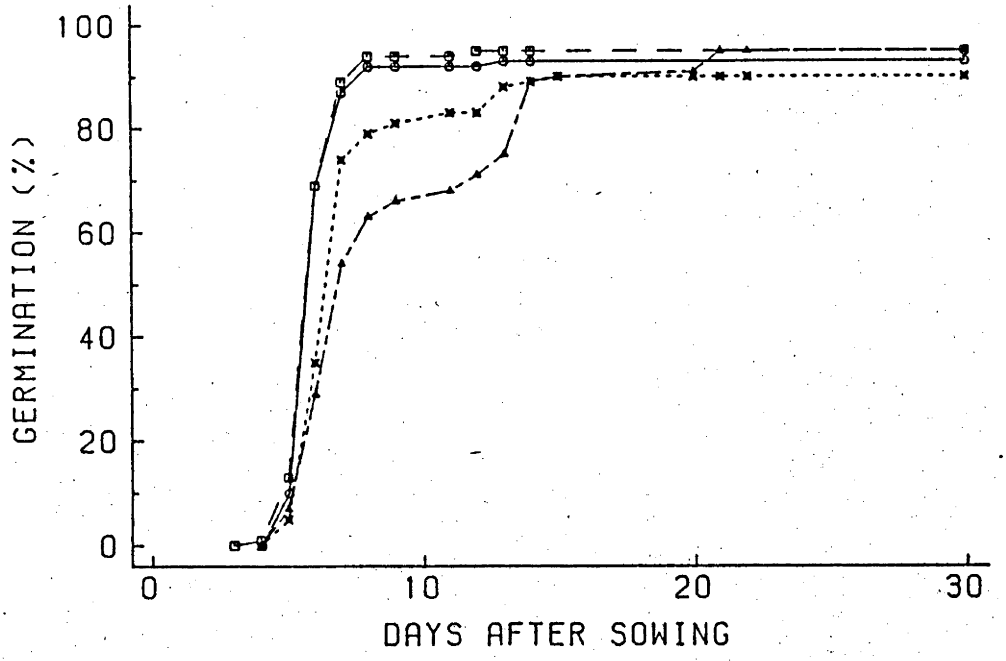


Figure 7.7 The effect of storage time on germination of E. incrassata seed (n = 100 seeds)

Pre-1980 2yr storage - dashed line, open symbols
Pre-1980 1yr storage - solid line
Pre-1980 .3yr storage - dotted line
1980 .3yr storage - dashed line, closed symbols

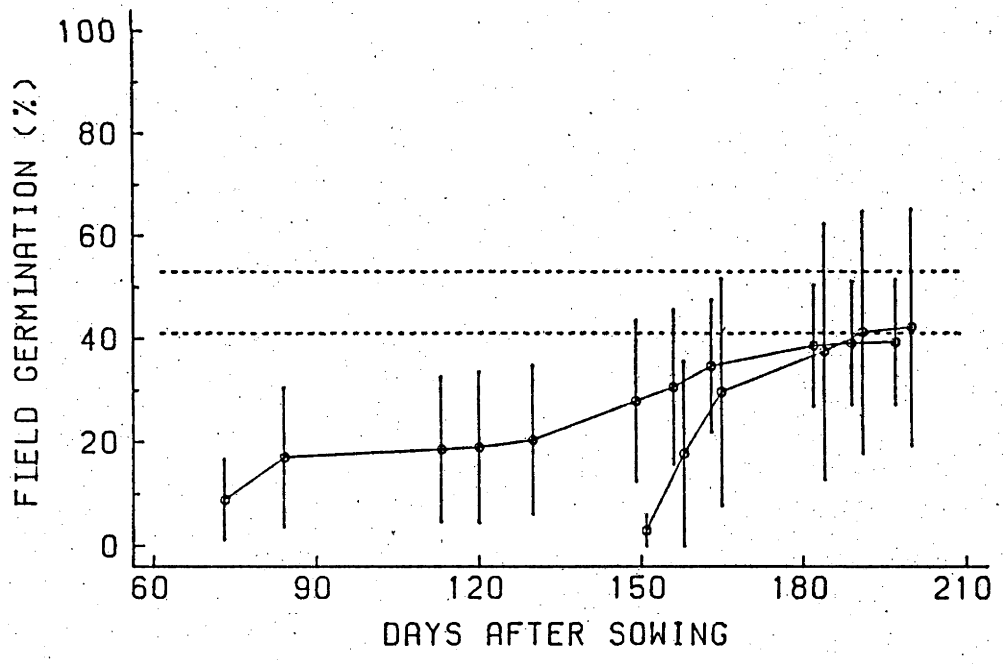


Figure 7.8 Minimum field germination (April 1980 to August 1980) (bars represent 95% confidence limits) (n = 7 x 100 seeds)

Note: The dashed lines represent upper and lower 95% confidence limits for laboratory germination of seeds sown in soil (7.2.2.3)

Comparisons between the number of emergent seedlings for each treatment on a particular day and the mean number of emergents from all samples on that day were made for the period from day five to day nine and for day thirty-six following sowing (Table 7.11).

Table 7.11 The effects of storage time on E. incrassata seed germination (filter paper substrate)

No. of days after sowing	Mean number of germinants	$X^2_{(3)}$	P
5	8.75	4.200	>.1
6	50.50	27.465	<.001***
7	76.00	10.237	<.025*
8	82.00	7.488	>.05
9	83.25	5.943	>.1
36	92.75	0.353	>.9

Significant differences occurred between the number of germinants from seeds of different storage age on the sixth and seventh days following sowing of the seeds (Table 7.11). Germination differences between treatments were not statistically significant after day seven.

Seeds of E. incrassata, stored in an air-dried state under laboratory conditions, exhibited higher initial germination rates with increased storage time. The difference between germination rates of seeds of different storage age decreased with germination time. There

was no significant decrease in total percentage germination of E. incrassata seeds stored over a period of two years under laboratory conditions. Seeds from eight month old, green capsules exhibited a similar total percentage germination to seeds from mature capsules which were at least two years old.

The total germination percentages for E. incrassata seed buried in soil at the field sites for periods of up to 300 days are presented in Table 6.11. Conditions appropriate for field germination occurred between 120 days and 200 days storage time, resulting in considerable 'in situ' germination of buried seed (see Section 7.4.1.2). Although no field germination was observed in the two quadrats which were sampled at 300 days, the possibility of germination and death of seedlings occurring in these two quadrats between monitoring periods cannot be excluded (see Section 7.4.1.2). Dry patches of soil were observed in adjacent mallee areas during the period of the present study, even when much of the surrounding soil was moist due to recent rainfall. Similar 'non-wettable' areas of soil may have prevented seed in these two quadrats from germinating in the field.

Comparisons were made between the total percentage germination of seed sown in soil samples and irrigated immediately under glasshouse conditions (Section 7.2.2.2), and the percentage germination of seeds buried in soil under field conditions for 120 days, 200 days and 300 days then irrigated under laboratory conditions (Section 6.6.4.3, Table 6.11). Comparisons were made using the test for comparison of percentages described by Sokal and Rohlf (1969, p608), and are shown in Table 7.12.

Table 7.12 Comparison of the percentage laboratory germination of seed stored in the field for 120 days, 200 days and 300 days (n=200) with seed which had never been stored in soil (n=1800; Section 7.2.2.2)

Comparison	ts	P
zero storage vs 120 days	7.495	<.001***
zero storage vs 200 days	1.896	.059
zero storage vs 300 days	3.282	.001**

E. incrassata seeds buried in soil in the field showed no significant loss of viability at 200 days storage time, but at 120 days and 300 days, they were significantly less viable than seeds which had never been stored in the soil (Table 7.12). Examination of the germination percentages for storage periods equal to, or greater than twenty-eight days, indicated a high variability of total germination (mean germination = 34 ± 8%; Table 6.11). This variability is further evident from the standard deviations for the minimum field germination recorded between 60 days and 200 days storage time (mean germination= 39 ± 13%; Table 6.11) and the germination for seeds of zero soil storage time (Mean = 47 ± 8%, Section 7.2.2.2). Possible reasons for variablity of germination in the soil have been discussed in Section 7.2.2.2. It should be noted that although the observed variations in germination may have been due to either a loss of viability of soil stored seed or variations in the soil environment, it is also possible that undetected field germination may have influenced this result (see Section 7.4.1).

In summary, it appears that fully-developed seeds of E. incrassata may retain high viability for up to two years storage time under low humidity laboratory conditions, and for up to 300 days storage time when buried in soil in the field. It is likely that prolonged soil storage under field conditions is contingent on buried seeds remaining relatively dry. Burial in areas of 'non-wettable' soil may be important in promoting long-term soil storage of seed. Most seed buried in soil in the field germinated readily in winter when the soil moisture levels remained high and temperatures were generally low (<20°C) (Chapter 3). E. incrassata seeds are non-dormant under these conditions (Section 7.3.2). Seeds resulting from a flowering period in the summer of 1979/80 were apparently mature by August 1980 and showed a high viability of fully-developed seeds.

7.4 Field germination

7.4.1 Field germination of buried and exposed seed

7.4.1.1 Introduction

As part of the experiment described in Section 6.6.4, a series of $0.25m^2$ quadrats, each containing one hundred E. incrassata seeds buried at about 1.0cm depth, were set up in February 1980 in a stand of unburnt mallee. At the same time, two large quadrats in which E. incrassata seed had been broadcast onto the soil surface, were established in an adjacent area (see Section 6.6.4.2).

Conditions suitable for seed germination occurred at the field sites during the period April 1980 to August 1980 and resulted in field germination of both buried seed and seed sown on the soil surface. This

section describes the results of monitoring field germination in both sets of quadrats.

7.4.1.2 Methods

Section 6.6.5.2 describes the manner in which both types of quadrats were set up.

Following the onset of germination of buried seed in April 1980, the numbers of germinants in each $0.25m^2$ quadrat were monitored twice-weekly during each field trip until August 1980. Dead seedlings, necrotic seedlings and seedlings which had been grazed were counted and removed at the end of each monitoring period.

The difference between the total number of seedlings present at the end of one field trip and the start of the next field trip was assumed to represent the total number of new germinants (or the total number of deaths when the difference was negative) occurring over that period. The germination data for each quadrat therefore represents a minimum estimate of field germination, and does not take into account seedlings which germinated and disappeared between monitoring periods. Instances where germination and death of two or more seedlings had occurred in parallel, resulting in a zero net change in the total number of seedlings, were not included either.

Germination commenced in the two larger quadrats containing surface-sown seed sometime prior to the June 1980 field trip. These two quadrats were carefully examined for new germinants at weekly intervals during the field trips in June 1980, July 1980 and August 1980. Each germinant was marked with a wire peg so that it could be easily relocated.

Grazing of new germinants was observed in April and May 1980. To investigate the effects of herbivore grazing on newly-germinated seedlings, six 0.25m^2 quadrats containing buried seed were set up as described in Section 6.6.5.2. These quadrats were established in early June 1980 and were located close to the 0.25m^2 quadrats established in February 1980 (see above). Three of the quadrats were enclosed with a 1.0cm mesh wire cage designed to exclude all large vertebrate herbivores but to allow access by invertebrate herbivores; the remaining quadrats were left exposed as controls.

The number of germinants and the number of grazed seedlings in each quadrat were monitored twice weekly during the July 1980 and August 1980 field trips. The germination data for the quadrats represent only a minimum estimate of field germination (see above).

7.4.1.3 Results and discussion

The mean minimum percentage germination of seeds buried in soil in the field was similar to the percentage germination of seeds sown in soil under laboratory conditions (Figure 7.8). Germination in the field took place over a longer period (>120 days) than the laboratory samples (<35 days). Low temperatures during June 1980 and July 1980 (see Figure 3.4) may have brought about the slower rates of germination observed in the field. Only three raindays occurred between 24 April 1980 and 4 June 1980, resulting in drier conditions in the surface soil, and causing the low germination rates in May and June 1980 (Figure 7.9). Uneven distributions of soil moisture may also have delayed germination at some sites (see Section 7.3.6.3).

Germination in the six 0.25m^2 quadrats set up in June 1980 had commenced prior to the July 1980 field trip. By the end of monitoring in August 1980, the mean minimum percentage germination was similar to

that measured for the $0.25m^2$ quadrats set up earlier in the year (Figure 7.8).

No grazed seedlings were detected in any of the six quadrats set up in June 1980. There was no difference in the number of germinants between the control quadrats and the quadrats with exclosures ($t_{(2)}=0.509$; $P>0.5$). The number of seedlings grazed during June 1980, July 1980 and August 1980 in the quadrats established in February 1980, fell dramatically in comparison with the high number of seedlings grazed during April 1980 and May 1980 (Figure 7.9). This decrease is also reflected in the absence of grazing from quadrats established in June 1980. It is likely that much of the grazing damage incurred in April 1980 and May 1980 was caused by invertebrate herbivores, since no signs of the presence of larger animals (e.g. tracks or dung) were seen near the quadrats, and the damage was often consistent with previously-observed insect grazing damage. The observed decrease in grazing damage between June 1980 and August 1980 may have been due to cooler temperatures reducing the activity of insect herbivores.

Mortality of new germinants due to factors other than insect herbivores was observed (Figure 7.9). It is likely that difficulty in establishing, or damage due to pathogen attack, were responsible for some of this mortality. No evidence of frost damage was observed during the study period (cf. Parsons 1968) although the presence of heavy canopies overhead and other site factors (e.g. elevation) may have reduced the frost effect. Monthly totals of the number of surviving seedlings are also included in Figure 7.9. These totals represent net changes in the number of germinants due to new germination, herbivory and other causes of mortality. It is apparent from the survivorship totals that despite early mortality, germination of seed buried in soil in unburnt areas continued through winter.

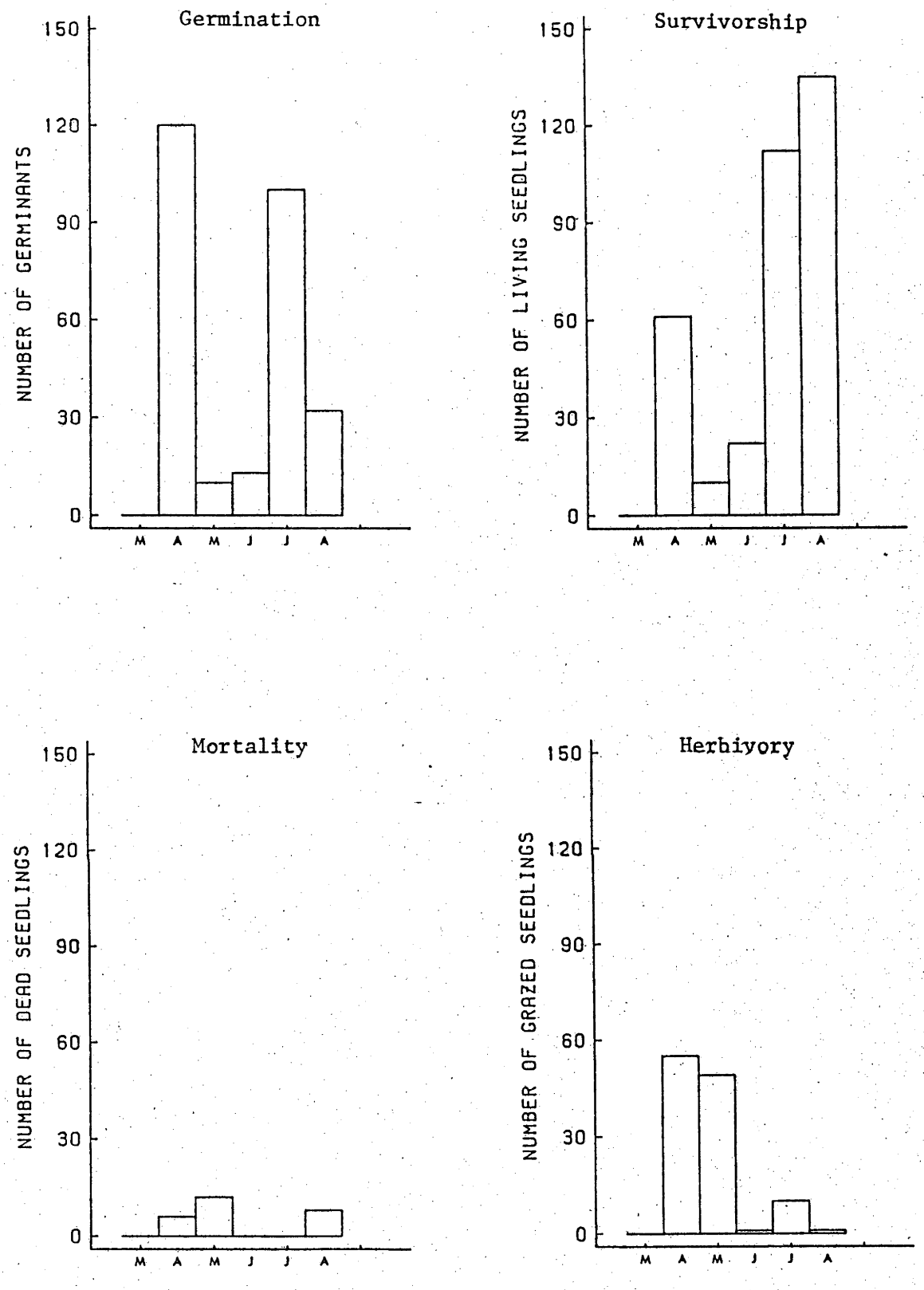


Figure 7.9 Field germination rates, and survivorship of new germinants from seed buried in soil in a long-unburnt stand of E. incrassata in 1980 (n = 7 x 100)

A total of eighty-four germinants were found in the quadrats with surface added seed during the period from April 1980 to August 1980. Sixty seedlings were located in the outer annular quadrat and twenty-four in the inner circular quadrat (see Section 6.6.5); these corresponded to seedling densities of 0.48 seedlings m^{-2} and 0.85 seedlings m^{-2} respectively.

7.4.2 Naturally-occurring germination

7.4.2.1 Introduction

There was no soil storage of E. incrassata seed in the unburnt stands examined (Section 6.5). However, a light seed rain from fecund canopies occurred throughout the year (Section 6.4), resulting in the occasional presence of viable seed on the soil surface (Section 6.5, Table 6.5).

Seed sown in February 1980 in the soil in long-unburnt mallee stands was found to germinate under field conditions during autumn 1980 and winter 1980 (Section 7.4.1). It therefore seemed likely that natural germination of seed falling from fecund canopies might also be occurring during this period. To investigate this possibility, several unburnt stands of E. incrassata adjacent to the field sites were searched for naturally-occurring germinants.

7.4.2.2 Methods

Three unburnt areas of E. incrassata situated immediately west of the burnt sites and separated from each other by distances of about 3km were examined for seedlings. The stands were examined weekly during the June 1980, July 1980 and August 1980 field trips. Each of the areas (approximately 1 ha) was searched using a series of parallel 1m wide

transects. The seedlings found were numbered and marked with a wire peg to facilitate relocation.

In each of the areas mentioned above, the most dense site of seedling recruitment was selected and a series of circular quadrats of 5m radius were marked out so as to include the majority of seedlings. These quadrats were used to map the position of seedlings and to obtain an estimate of maximum seedling density.

A broad-scale estimate of the density of germinants in the unburnt region west of Lake Albacutya was obtained using a series of eight, parallel 1m wide transects, each 1.1km in length. The transects were oriented at 180° and were separated from each other by 30m. Seedlings located within the transects were counted.

A more wide-ranging survey of E. incrassata stands north-west of Lake Albacutya and in Wyperfeld National Park, was also conducted in August 1980. Ten stands containing fecund specimens of E. incrassata were examined using short 1m wide transects as described above. The stands were located along a road transect approximately 40km in length.

7.4.2.3 Results and discussion

Naturally-occurring germinants were first detected in early June 1980. By the end of August 1980, a total of 293 germinants had been located in three stands of fecund E. incrassata representing a density estimate of ca 10^2 seedlings ha^{-1} (Table 7.13).

Table 7.13 Total numbers of natural germinants located in three 1 ha areas of unburnt mallee between 7 June 1980 and August 1980.

	Total number of seedlings located			
Month	Area 1	Area 2	Area 3	Total
June 1980	64	20	20	104
July 1980	102	35	28	165
August 1980	163	81	49	293

Maximum seedling densities for the three areas examined varied between 0.2 seedlings m^{-2} and 0.4 seedlings m^{-2}. Sites of maximum density were located under fecund canopies.

In the broad-scale survey for new germinants, conducted in unburnt stands of E. incrassata west of Lake Albacutya, a total of twenty-seven germinants were found. The total area surveyed amounted to 8800m : the recruitment rate over large areas of unburnt mallee was therefore estimated to be ca 30 seedlings ha^{-1}.

New germinants were found in seven of the ten E. incrassata stands examined during the wide-ranging survey conducted over a 40km road transect in mallee areas north-west of Lake Albacutya. Owing to time limitations, no attempt was made to quantify germination densities in the stands examined. However, the occurrence of germinants in most stands indicates that natural germination of E. incrassata seeds was a relatively common event in unburnt areas during 1980.

The 293 new germinants, located between June 1980 and August 1980 and marked with wire pegs to facilitate relocation (Section 7.4.1.2), were re-examined in early December 1980. All new germinants were dead. A brief survey of surrounding areas and of the quadrats in which germinants had been recorded from both buried seed and surface-sown seed in August 1980, also showed that no seedlings had survived. Apparently the seedlings which had germinated during winter 1980 had been unable to establish, and had perished by the end of spring 1980. It was not possible to investigate likely causes of mortality since the program of field work had been brought to a conclusion.

7.5 Summary and general discussion

Fully-developed E. incrassata seeds exhibited high (>80%) laboratory germination rates on a moist filter paper substrate, but lower (ca 47%) laboratory germination rates when sown in soil. Germination responses of seeds sown in soil collected from unburnt stands were highly variable, both between replicate samples (mean = 47 $\pm$ 8%), and between similar samples in experiments conducted at different times (germination range of 21% to 75%).

High temperatures (30°C) and a twelve-hour photoperiod under an alternating temperature regime of 30°/20°C inhibited germination of E. incrassata seeds. Optimal germination occurred at a temperature of 20°C. Lower temperatures (<20°C) increased the time taken for germination to occur, but did not influence the final percentage germination. Exposure to light had no effect on germination at constant temperatures between 5°C and 30°C, or under an alternating temperature regime of 20°/10°C.

Sowing depths of between 0.1cm and 1.0cm had no effect on either rate of germination or final germination percentages. A sowing depth of 2.0cm caused a small but significant reduction in both rate of germination and the total number of germinants. Seeds mixed through the soil profile to 2.0cm depth showed no significant decrease in germination. Seeds sown on the soil surface exhibited slower rates of germination, but similar final germination percentages to seeds sown at depths of 1.0cm and above. Optimal sowing depth was between 0.1cm and 1.0cm.

Heat treatment (to 180°C) of soil resulted in increased rates of germination and an increase in the total number of germinants from seeds sown after treatment. Enhancement of germination occurred in heated soil under temperature regimes of 20°/10°C and 30°/20°C, although some inhibition of germination was evident under the higher temperature regime. The presence of ash also had a stimulatory effect on germination. Both of these factors are associated with fire-effects on soil and the creation of an ashbed. A similar enhancement of germination was observed in soil collected from a recently-burnt mallee area. Fire-associated changes to the surface soil are thus important in promoting recruitment in recently-burnt areas by causing enhanced germination.

E. incrassata seed may remain stored under laboratory conditions for periods of at least two years without significant loss of viability. Seed buried in soil in the field shows a small but statistically significant initial decrease in viability, but no further loss of viability occurs for up to 300 days storage time. However, E. incrassata seeds are non-dormant under autumn/winter/spring conditions and high soil moisture levels during these months probably cause most seeds present in the soil to germinate.

Germination of both buried seed and seed added to the soil surface of unburnt stands occurred between April 1980 and August 1980. Surveys of unburnt areas indicated that natural germination of E. incrassata seed also occurred during this period; densities of natural germinants were estimated at $<10^2$ ha^{-1}. Natural germination was widespread, occurring in areas separated by up to 40km, but was largely confined to fecund stands of E. incrassata. No germinants survived beyond early December 1980.

Germination of E. incrassata seeds on the soil surface is inhibited in summer as a result of both high temperatures and exposure to light, even when soil moisture levels are high. However, the milder temperatures of autumn, winter and spring, may result in widespread germination as soon as soil moisture levels are high enough. The effects of temperatures below 5°C on germination were not investigated in the present study, but it is probable that germination rates become slower as the temperature drops below this level.

Fire-associated changes to the soil resulted in an increase in the rate of germination and in the total number of germinants obtained from seed sown after treatment. This increased germination response is likely to be a significant factor contributing to successful post-fire recruitment of mallee eucalypts. Higher rates of germination may enable seeds in burnt soil to germinate in favourable periods too short for germination of seeds to occur in unburnt soils. A high total percentage germination is likely to be important since there are often relatively few sites suitable for long-term establishment, and higher numbers of germinants would increase the probability of some seedlings occurring at these sites. Fire-induced changes are also important for successful seedling establishment following germination; the effects of the 'ash bed' response on seedling growth and vigour have been widely reported in

the literature.

There appears to be no allelopathic or other factors strongly inhibiting germination of E. incrassata seed in the soils of unburnt stands. Field germination rates of artificially-sown seed were similar to laboratory germination rates. The density of germinants resulting from surface-sown seed applied at likely post-fire seed densities to the soil of an unburnt E. incrassata stand were high (up to 0.85 seedlings m^{-2}). Similarly the densities of natural germinants under fecund canopies were occasionally high (0.2 to 0.4 seedlings m^{-2}). The density of natural germinants occurring in unburnt stands of E. incrassata in August 1980 ($<10^2 ha^{-1}$) was considerably lower than seedling densities estimated following the December 1977 fire at Lake Albacutya (ca 10^4 seedlings ha^{-1}, see Chapter 4). Fire-associated changes to the soil causing enhanced germination, together with a greatly increased seed population in the soil following the fire are responsible for this difference.

CHAPTER EIGHT

MALLEE DYNAMICS: A SYNTHESIS

CHAPTER 8

MALLEE DYNAMICS: A SYNTHESIS

8.1 Introduction

The model described in Section 2.7 (see Figure 2.1) depicts both the life stages through which mallee genets are likely to pass, and the processes which control the rate of movement of genets between successive life stages. Chapters 4 and 6 describe investigations into the number of genets present at different life stages in a population of E. incrassata, part of which had been recently burnt. Investigations were also made into factors controlling some of these processes (Chapters 5, 6 and 7). Particular emphasis was placed on causes of mortality during the early life stages, and on the factors controlling recruitment of genets into the population. The present chapter discusses each of these investigations in terms of the life stages represented in the model in an attempt to provide an integrated view of mallee dynamics. While the interpretations of mallee dynamics discussed here are strictly applicable only to the population of E. incrassata investigated at Lake Albacutya, it is likely that they also apply to other mallee populations.

Recruitment of E. incrassata genets is confined to disturbed sites, and in particular to recently-burnt areas. In long-unburnt areas, successful recruitment is limited by the absence of soil seed stores, the rapid removal of most newly-fallen seed from the soil surface, and the apparent inability of newly-germinated seedlings to establish.

Climatic factors and changes in the relative abundance of both predators and pollinators impose a stochastic element on flowering and seed production despite an underlying flowering rhythm of two to four years. Seed of the mallee E. incrassata is stored in fruits in the canopy and released as a light intermittent seed rain over a period of several years. The amount of seed stored in the canopy of long-unburnt stands is highly variable both spatially and temporally.

Newly-fallen seeds are removed from the soil surface by seed harvesting ants. Seed removal is rapid (half-life of an isolated seed is less than 2 days) and affects most newly-fallen seed in unburnt situations. Harvesting activities in unburnt sites were found to be spatially variable and areas of low or zero removal activity occurred: these are areas where seed may remain on the soil for periods long enough for germination to take place.

Natural germination of E. incrassata seed occurred in unburnt stands during the cooler months of 1980, and probably resulted from either newly-fallen seed, or seed present in areas of low harvesting activity. Rates of natural germination were low ($<10^2$ $ha^{-1}yr^{-1}$) and confined to fecund stands. However, conditions in unburnt stands were apparently not conducive to seedling establishment in 1980, and of 293 natural germinants monitored, none survived to the beginning of summer.

Fire in a mallee stand apparently results in mass release of all canopy seed reserves. A sudden release of E. incrassata seed onto the soil surface of an unburnt stand at probable post-fire densities resulted in the establishment of a seed store in the soil. This phenomenon is thought to be due to predator satiation (Janzen 1969) caused by a sudden increase in food resources. A similar situation may occur after a fire in natural mallee stands.

Seeds of E. incrassata can remain in the soil of unburnt stands in a viable condition for at least one year. Both laboratory and field germination rates of E. incrassata seeds in soil are variable, and are lower (<50%) than germination rates on moist filter paper (>80%). High temperatures (ca 30°C) inhibit germination. Optimal germination occurs at ca 20°C. Lower temperatures (down to 5°C) increase the time taken for germination to occur, but do not influence the total number of germinants; field germination is therefore restricted to the cooler months of the year. A consideration of climatic data for the study sites (Chapter 3) indicates that conditions suitable for germination occur during autumn, winter and spring in most years. Thus E. incrassata seeds present in the soil are likely to germinate in most years.

Fire-induced changes to the soil have a stimulatory effect on germination of seed added following the fire. The presence of ash and the effects of heat on soil, both result in faster rates of germination and an increased total number of germinants (ca 60%) in seed sown after the treatments.

Initial recruitment of seedlings in a recently-burnt area was estimated to be 10^4 seedlings ha^{-1}. By contrast, in the absence of fire, natural seed germination during favourable winter conditions was

estimated at less than 10^2 germinants ha^{-1}. Fire is therefore an important factor facilitating seedling recruitment since it both creates an ashbed capable of sustaining rapid germination of large quantities of seed, and results in the establishment of seed populations in the soil. Fire is also crucial for successful establishment of seedlings. Although new germinants were found in unburnt stands in 1980, none of these survived more than a few months. It is possible that the conditions limiting establishment, which occurred during 1980, were exceptional. However, the widely-noted absence of seedlings from unburnt stands (Chapter 1) confirms that establishment in the absence of fire is a rare event.

Limitations in the availability of resources, particularly soil moisture during summer, are responsible for widespread seedling mortality in recently-burnt areas (Chapters 4 and 5). Resource limitations in the upper levels of the soil surface are probably even more extreme in unburnt stands. Evapotranspirational demand for soil moisture from established vegetation is high during prolonged dry periods in summer (Specht 1957b). Fire has the effect both of releasing nutrients previously incorporated in litter and plant ramets, and of temporarily eliminating the demands placed on soil nutrient and moisture resources by the vegetation. Several years may elapse before community evapotranspirational demand on soil moisture returns to preburn levels (Zimmer 1940b). The reduction in competition for limiting resources as a result of fire is probably crucial for seedling establishment.

Successful recruitment does not follow every fire in mallee populations. Observation of a large number of populations burnt within the past fifteen years indicated that only a small proportion of fires resulted in recruitment. The high temporal and spatial variability of canopy-stored seed reserves leads to a high probability that some stands

will be in a state of low fecundity at the time of a fire, resulting in limited recruitment. E. incrassata seeds are non-dormant under most conditions (Scott 1979) and climatic conditions suitable for germination occur in most years. It is therefore probable that germination of fire-induced soil seed reserves follows the majority of fires in mallee, but that extreme conditions, either frosts during winter (Parsons 1968a) or high temperatures and low soil moisture levels during the following summer, result in death of all germinants. Conditions in the year following a fire are crucial in determining whether successful recruitment takes place. Both the time of the year when a fire occurs, and the time when conditions suitable for germination arise may be important, since older seedlings which germinated early in the previous autumn are likely to be better established, and thus have a greater tolerance for summer conditions than seedlings which germinated in late winter or spring.

8.3 Mortality

The survival rate of E. incrassata genets varies between different life stages.

Mortality of seeds (new genets) is extremely high. A fecund E. incrassata adult may produce between 10^5 and 10^6 seeds during its lifetime. Few ($<10^3$) of these germinate and very few ($0-10^1$) ever reach maturity. Most seeds are removed or destroyed by predators or pathogens either before or after dispersal.

Mortality of seedlings prior to establishment is also high. In this study, mortality rates of emergent seedlings and established seedlings were included in an estimate representing a composite

'seedling' life stage. Seedling mortality rates were high (64% yr^{-1}) and confined to summer. Juvenile mortality was similarly high (45% yr^{-1}) and confined to summer. Mortality of new genets over the first two years of life was estimated at ca 75%. By contrast, mortality rates of long-established adults measured over the same period were very low (ca 0.6% in two years). These correspond to the Type III survivorship curve described by Deevey (1947).

Radiocarbon dating of mallee lignotuber tissues demonstrated ages of less than 200 years (Chapter 2, Appendix 1). Age estimates for other Eucalyptus species have indicated life-spans of up to 400 years (Ogden 1978). The mallee lignotubers used for the ^{14}C age determinations were large, healthy specimens, and it is probable that their expected life span would have exceeded the demonstrated radiocarbon ages. Although the above investigations do not preclude the possiblity that mallee genets may attain great age (see Chapter 2), the evidence presently available indicates a likely life-span for mallee genets of ca 200-400 years.

It is probable that mallee eucalypts, like many long-lived perennial plants, have constant, low mortality rates over the greater part of their life-span. However adult mortality in recently-burnt areas was considerably higher (ca 2.5% yr^{-1}) than in adjacent unburnt stands. It is therefore likely that the recurrence of fire in mallee populations results in periods of higher mortality, corresponding to a series of small drops on the long, flat 'tail' of the Type III survivorship curve. Cheal et al. (1979) estimated that large fires in the mallee of north-western Victoria recur at intervals of about twenty years. Calculations made of genet depletion rates based on measured mortality rates from unburnt and recently-burnt stands and using a twenty-year fire regime are included in Table 8.1a. These calculations

Table 8.1 Calculation of depletion rates of adult mallee genets

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a. Measured mortality rates

Assumptions:

1. mortality rate of unburnt adults is 0.3% yr^{-1}
2. mortality rate of recently-burnt adults is 2.5% yr^{-1}
3. mortality rates return to 0.3% yr^{-1} two years after a fire
4. fires recur at 20 year intervals

Survivorship (%)

after 100 years = 59% ($.975^{10} \times .997^{90} \times 10^2$)

after 200 years = 35%

after 400 years = 12%

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b. Estimated mortality rates

Assumptions:

1. mortality rate of unburnt adults is 0.6% yr^{-1}
2. mortality rate of recently burnt adults is 5.0% yr^{-1}
3. mortality rates return to 0.6% yr^{-1} two years after a fire
4. fires recur at 20 year intervals

Survivorship (%)

after 100 years = 35% ($.95^{10} \times .994^{90} \times 10^2$)

after 200 years = 12%

after 400 years = 1.5%

---

indicate that 12% of a cohort of adults would remain alive after 400 years. Considering that the measurements on which these calculations were based were made over a very short time period (2 years), and that the particular two year measurement period coincided with a recruitment phase (i.e. years of 'good' conditions), it was considered probable that mortality rates of adults in less clement years would be higher. Therefore, depletion rates based on increased mortality estimates were also calculated and are included in Table 8.1b.

Depletion rates based on both actual and projected mortalities (Table 8.1) support the longevity estimates obtained from ^{14}C age determinations, and indicate that mallee genets may have a similar life-span to other species of Eucalyptus (i.e. 200-400 years).

8.4 Population structure

Survival of new germinants of E. incrassata in recently-burnt areas appears to be largely contingent on the availability of resources, particularly soil moisture. A similar situation is likely to occur in unburnt stands. Availability of certain resources such as soil nutrients increases as a result of fire, and decreases with time as the biomass of the vegetation increases and nutrient recycling is established (Burrows 1976). Soil moisture on the other hand is dependent on rainfall, and thus is highly variable. The timing and extent of rainfall events following post-fire seed shed largely determine whether germination and subsequent establishment occur. Post-fire reduction of community evapotranspiration is an important factor influencing soil moisture levels, and therefore influences establishment.

The increased mortality of adults which occurs following fire is likely to enhance the establishment prospects of new genets. Death of an adult relinquishes space, removing the dominance over resources contained within that space. This increase in resource availability may be crucial in facilitating the long-term success of newly established genets. If mallee populations were generally close to the carrying capacity, as determined by availability of resources during extreme summers, then a gradual one-to-one replacement sequence would occur. However, the restriction of recruitment to situations in which seasons of high rainfall follow a fire in a fecund stand imposes a high degree of stochasticity on the introduction of new genets into the population. For the perpetuation of mallee populations, successful recruitment must occur at least once every 200-400 years, and may occur more frequently. Mortality of adults between recruitment events may result in stands well below carrying capacity, and thus provide scope for the introduction of larger cohorts of new genets. The number of new genets which will be successfully incorporated into the population from any recruitment event is probably variable. As a result, mallee populations may have complex age structures. The relationship between adult mortality, the formation of 'resource gaps' in the population and the size of cohorts recruited into the population is a possible subject for future investigation, but would require a longer (5-10 year) study.

8.5 Selection in mallee populations

Recurrent fire and seasonal limitations of soil moisture influence reproduction and survivorship of mallee genets, and therefore constitute important selection forces acting on mallee populations.

The retention of the lignotuber as a significant part of the adult growth form is an adaption imparting a high degree of resilience to mallee genets. The lignotuber enables mallee genets both to survive recurrent fires, and to regenerate new stems within a short period of time, thus retaining dominance over a particular resource space. The regenerative capacity of the lignotuber also ensures that mallee genets may survive for long enough to be able to contribute new genets to another generation and therefore enables populations to persist despite the stochastic influences on recruitment.

Recurrent fire, the effects of ants in reducing the presence of seed in the soil, and the inability of new germinants to establish in unburnt stands, together represent strong selection forces favouring the retention of seed reserves in the canopy. The stochastic nature of fire occurrence means that individuals which retain seed in the canopy for shorter periods of time are less likely to contribute new genets to future seedling cohorts.

Drought represents an important selection force acting on mallee genets. Summer seasons are characterized by long, dry spells and survival of new genets is largely determined by their ability to either avoid or tolerate drought stress. The high mortality rates observed amongst new genets of E. incrassata during this study were primarily a result of soil moisture limitations. Both physiological and morphological adaptations for avoiding or tolerating drought effects are therefore highly selected for amongst mallee genets. Evidence for the existence of both types of adaptations in mallee genets is discussed in Section 5.4.

Established genets of E. incrassata growing on sand dunes were able to maintain high leaf conductance rates and high internal water potentials during a prolonged summer drought whereas surrounding juveniles experienced very low water potentials. An important aspect of successful establishment of E. incrassata genets probably involves the rapid development of deep root systems; individuals with shallow root systems would be more drought prone and thus less likely to survive. Parsons (1968c) has measured relatively high growth rates in E. incrassata compared to other mallee species. High growth rates enable faster root penetration, thereby providing an enhanced drought avoidance ability for plants growing on sand dunes. The slower growth rates measured by Parsons (1968c) for other mallee species (e.g. E. diversifolia) occurring on shallow soils with lower water availability enable these species to avoid drought stress by reducing water usage. Selection for fast or slow growth rates of mallee genets is thus dependent on particular soil conditions. The effects of growth rates on the success of mallee genets within a population is another possible area for future research.

8.6 Fire and stability of mallee populations

It is apparent from the foregoing sections that recurrent fire is of crucial importance to the perpetuation of mallee eucalypt populations. Mallee populations have evolved under the influence of recurrent fire and possess mechanisms for survival and recruitment which are especially adapted to the presence of fire. In the terminology of the scheme proposed by Noble and Slatyer (1980): mallees have a short-lived seed pool which can survive and germinate immediately after

a disturbance (C); they have an ability to survive disturbances, but subsequently lose all of their recruitment capacity for a short time (V); and they are able to establish and grow at a site immediately after a disturbance but cannot establish as the competition for resources increases (I); they are thus classified as VI species. This scheme predicts that for VI species, "an interval between disturbances (eg. fire) greater than the life span of individuals .... leads to local extinction" (Noble and Slatyer 1980).

From the results presented in previous sections, it is obvious that in the long-term (>400 years) absence of fire, senescence and genet mortality would cause a mallee population to fall well below carrying capacity, and perhaps enable establishment of new genets to occur in the resultant 'gaps'. However, the reduction of soil seed reserves by seed harvesters and the effect of other species in limiting available resources may preclude gap recruitment in senescent populations of sufficient extent to perpetuate the population. In the absence of seed harvesting it is probable that recruitment of this type would be more important.

In the absence of fire, mallee eucalypts would become a much less dominant component of the vegetation and might even be replaced by invading species better able to establish in unburnt situations. The latter species would possibly be fire-sensitive, and thus be presently excluded by the existing fire regime. Mallee populations are apparently stable only when subjected to a regime of recurrent fire.

The prediction derived from the successional scheme of Noble and Slatyer (1980) seems to be reliable. However, it is possible that one of the premises on which the prediction is based (viz: mallees cannot establish as the competition for resources increases) is not strictly

accurate since seed harvesters may be crucial in limiting gap recruitment.

8.7 The life stage approach in demographic studies

The classification of genets in a population into life stages representing functionally distinct phases of the life-cycle was adopted in this study. This approach overcomes the problems associated with determining genet ages of long-lived perennial plants, necessary for an age-class or life table analysis, by providing a more pragmatic and perhaps more meaningful basis for a study of plant populations.

Due to dominance, suppression, site quality, and other factors there is often a range of size and fecundity represented amongst the genets comprising a plant population. The age of genets is therefore not a good parameter upon which to base a demographic study, since individuals of the same age may differ considerably in these qualities and hence differ in their importance to the population (Rabotnov 1969). The use of a life stage approach is one way of overcoming this problem: the demographic data obtained using life stages may thus be more useful than age class data in investigating population processes.

The life stage approach has been largely used by Russian workers in previous demographic studies; a brief review of some of this work may be found in Harper and White (1979). A modified version of the life stage approach, as applied to a mallee population in the present study, enabled meaningful demographic data to be collected in a short time, and provided a sound basis for an interpretation of mallee population dynamics. It is likely that this approach will prove useful in demographic studies of other long-lived perennial species.

REFERENCES

Andersen, A.N. (1980) Seed-removal by ants at a mallee site in northwestern Victoria. BSc(hons) Thesis, Monash Univ.

Ashton, D.H. (1975) Studies of flowering behaviour in Eucalyptus regnans F. Muell. Aust. J. Bot. 23: 399-411.

Ashton, D.H. (1979) Seed harvesting by ants in forests of Eucalyptus regnans F.Muell. in central Victoria. Aust. J. Ecol. 4: 265-277.

Barbour, M.G. and Lange, R.T. (1967) Seed populations in some natural Australian topsoils. Ecology 48: 153-155.

Beadle, N.C.W. (1940) Soil temperatures during forest fires and their effect on the survival of vegetation. J. Ecol. 28: 180-192.

Beadle, N.C.W. (1948) The vegetation and pastures of western New South Wales. Government Printer, Sydney.

Blake, G.R. (1965) Bulk density. In: Methods of Soil Analysis. Part 1. Physical and Mineralogical Properties. (Editor in chief: C.A. Black) pp 375-377. Amer. Soc. Agron., Washington, U.S.A.

Boden, R.W. (1957) Some aspects of seed dormancy in Eucalyptus. Aust. For. 21 (2): 81-85.

Boland, D.J., Brooker, M.I.H. and Turnbull, J.W. (1980) Eucalyptus seed. C.S.I.R.O. Australia.

Bond, H.W. and Brown, W.L. (1979) The exploitation of floral nectar in Eucalyptus incrassata by honeyeaters and honeybees. Oecol. 44: 105-111.

Boomsma, C.D. (1972) Native Trees of South Australia. Woods and Forest Dept., South Australia.

Bowler, J.M. and Magee, J.W. (1978) Geomorphology of the Mallee region in semi-arid northern Victoria and western N.S.W. Proc. R. Soc. Vict. 90:5-21.

Briese, D.T. (1974) Ecological studies of an ant community in a semi-arid habitat (with emphasis on seed-harvesting species). Ph.D. Thesis, Aust. Nat. Univ.

Briese, D.T. and Macauley, B.J. (1980) Temporal structure of an ant community in semi-arid Australia. Aust. J. Ecol. 5: 121-134.

Briese, D.T. and Macauley, B.J. (1981) Food collection within an ant community in semi-arid Australia with special reference to seed harvesters. Aust. J. Ecol. 6: 1-19.

Brown, J.H., Reichman, O.J. and Davidson, D.W. (1979) Granivory in desert ecosystems. Ann. Rev. Ecol. Syst. 10: 201-227.

Burbidge, N.T. (1952) The significance of the mallee habit in Eucalyptus. Proc. Roy. Soc. Qld. 62: 73-78.

Burrows, W.H. (1976) Aspects of nutrient cycling in semi-arid mallee and mulga communities. Ph.D. Thesis, Aust. Nat. Univ.

Carrol, E.J. and Ashton, D.H. (1965) Seed storage in soils of several Victorian plant communities. Vict. Nat. 82: 102-110.

Chattaway, M.M. (1958a) Bud development and lignotuber formation in eucalypts. Aust. J. Bot. 6: 103-115.

Chattaway, M.M. (1958b) The regenerative powers of certain eucalypts. Vict. Nat. 75: 45-46.

Cheal,P.D., Day,J.C. and Meredith, C.W. (1979) Fire in the National Parks of north-west Victoria. National Parks Service, Victoria.

Christensen, P. (1971) Stimulation of seedfall in karri. Aust. For. 35: 182-190.

Clifford, H.T (1953) A note on the germination of Eucalyptus seed. Aust. For. 17: 17-20.

Collatz, J., Ferrar, P.J., and Slatyer, R.O. (1976). Effects of water stress and differential hardening treatments on photosynthetic characteristics of a xeromorphic shrub, Eucalyptus socialis, F. Muell. Oecol. 23: 95-105.

Cowan, I.R. (1977) Stomatal behaviour and environment. Adv. Bot. Res. 4: 117-227.

Cowan, I.R. (1981) Coping with water stress. In: Biology of Australian Native Plants. (Eds. J.S. Pate and A.J. McCoomb). Univ. of W.A. Press, Perth.

Cremer, K.W. (1965a) How eucalypt fruits release their seeds. Aust. J. Bot. 13: 11-16.

Cremer, K.W. (1965b) Effects of fire on seedshed from Eucalyptus regnans. Aust. For. 29: 252-262.

Cremer, K.W. (1965c) Emergence of Eucalyptus regnans seedlings from buried seed. Aust. For. 29: 119-124.

Cremer, K.W. (1966) Dissemination of seed from Eucalyptus regnans. Aust. For. 30: 33-37.

Cremer, K.W. (1977) Distance of seed dispersal in eucalypts estimated from seed weights. Aust. For. Res. 7: 225-228.

Cremer, K.W., Cromer, R.N. and Florence, R.G. (1978) Stand establishment. In: Eucalypts for wood production.(Eds. W.E. Hillis and A.G. Brown) C.S.I.R.O., Australia.

Cremer, K.W. and Mount, A.B. (1965) Early stages of plant succession following the complete felling and burning of Eucalyptus regnans forest in the Florentine Valley, Tasmania. Aust. J. Bot. 13: 303-322.

Cunningham, T.M. (1957) Seed production and seed fall of Eucalyptus regnans F. Muell. Aust. For. 21: 30-39.

Cunningham, T.M. (1960) The natural regeneration of Eucalyptus regnans. Sch. For. Univ. Melb. Bull. No. 1.

Davidson, D.W. (1977) Foraging ecology and community organization in desert seed-eating ants. Ecology 58: 725-737.

Deevey, E.S. (1947) Life tables for natural populations of animals. Quart. Rev. Biol. 22: 283-314.

Doley, D., and Trivett, N.B.A. (1974) Effects of low water potentials on transpiration and photosynthesis in Mitchell grass (Astrebla lappacea). Aust. J. Plant Physiol. 1: 539-550.

Drake, D.W. (1975) Seed abortion in some species and interspecific hybrids of Eucalyptus from Australia. Aust. J. Bot. 23: 91-995.

Driessche, R. van den, Connor, D.J., and Tunstall, B.R. (1971). Photosynthetic response of Brigalow to irradiance, temperature and water potential. Photosynthetica 5: 210-217.

Eldridge, K.G. (1963) The effects of honeybees on seed production of Eucalyptus regnans. For. Comm. Vict. Tech. Pap. 13: 6-13.

El-Ghonemy, A.A. (1966) Soil - vegetation relationships for some major plant communities in south-western New South Wales. Ph.D. Thesis, Univ. of New England.

Ewart, A.J. (1908) On the longevity of seeds. Proc. Roy. Soc. Vict. 21: 1-210.

Farquhar, G.D., Dubbe, D.R. and Raschke, K. (1978). Gain of the feedback loop involving carbon dioxide and stomata. Plant Physiol. 62: 406-412.

Florence, R.G. (1964) A comparative study of flowering and seed production in six blackbutt (Eucalyptus pilularis) stands. Aust. For. 28: 23-33.

Floyd, A.G. (1966) Effects of fire upon weed seeds in the wet sclerophyll forests of northern New South Wales. Aust. J. Bot. 14: 243-246.

Foster, M.B. (1979) The ecology of Pinus radiata D.Don invading dry sclerophyll eucalypt forest in the A.C.T. Ph.D. Thesis, Aust. Nat. Univ.

Free, R.A. (1951) Germination and emergence of eucalypt seed when sown at depth. Aust. For. 15:115-120.

Fritts, H.C. (1976) Tree Rings and Climate. Academic Press, London.

Gardner, W.H. (1965) Water content. In: Methods of Soil Analysis. Part 1. Physical and Mineralogical Properties. (Editor in chief: C.A. Black) pp 92-96 Amer. Soc. Agron. Washington, U.S.A.

George, I. (1974) Hattah Lakes National Park regeneration area. 11th Rep. Sunraysia Nat. Res. Trust pp8-9.

Gill, A.M. (1975) Fire and the Australian flora: A review. Aust. For. 38: 4-25.

Gill, E.D. (1966) Geochronology of Victorian mallee ridges. Proc. Roy. Soc. Vict. 79 (2): 555-559.

Gill, E.D. (1971) Applications of radiocarbon dating. Proc. Roy. Soc. Vict. 84: 71-86.

Goodman, R.D. (1973) Honey Flora of Victoria. Dept. Agric., Vict.

Grant Taylor, T.L. and Rafter, T.A. (1963) N.Z. natural radiocarbon measurements I-V. Radiocarbon 5: 118-161.

Grose, R.J. (1960) Effective seed supply for the natural regeneration of Eucalyptus delegatensis R.T. Baker. Appita 13: 141-148.

Grose, R.J. and Zimmer, W.J. (1957) Preliminary laboratory studies on light requirements for the germination of some eucalypt seeds. Aust. For. 21: 76-80.

Grose, R.J. and Zimmer, W.J. (1958) Some laboratory germination responses of the seeds of river red gum Eucalyptus camaldulensis Dehn. syn. Eucalyptus rostrata Schlecht. Aust. J. Bot. 6: 129-153.

Hannay, A.K. (1965) Some aspects of the climate of the Victorian Mallee. Working Paper 65/3323. Bureau of Meteorology, Melbourne.

Harper, J.L. (1967) A Darwinian approach to plant ecology. J. Ecol. 55: 247-270.

Harper, J.L. (1977) Population Biology of Plants. Academic Press, London.

Harper, J.L. and White, J. (1974) The demography of plants. Ann. Rev. Ecol. Syst. 5: 419-463.

Harwood, C.E. (1976) Ecological studies of timberline phenomena. Ph.D. Thesis, Aust. Nat. Univ.

Hellmuth, E.O. (1971) Eco-physiological studies on plants in arid and semi-arid regions in Western Australia. III. Comparative studies on photosynthesis, respiration and water relations of ten arid-zone and two semi-arid zone plants under winter and late summer climatic conditions. J. Ecol. 59: 225-260.

Hett, J.M. and Loucks, O.L. (1971) Sugar maple (Acer saccharum Marsh.) seedling mortality. J. Ecol. 59: 507-520.

Hills, E.S. (1939) The physiography of north-western Victoria. Proc. Roy. Soc. Vict. 51: 297-320.

Hodgkinson, K.C., Harrington, G.N. and Miles, G.E. (1980) Composition, spatial and temporal variability of the soil seed pool in a Eucalyptus populnea shrub woodland in central New South Wales. Aust. J. Ecol. 5: 23-29.

Holland, P.G. (1967) Biomass and pattern in the ecology of mallee vegetation. Ph.D. Thesis, Aust. Nat. Univ.

Holland, P.G. (1968) Seasonal growth of field layer plants in two stands of mallee vegetation. Aust. J. Bot. 16: 615-622.

Holland, P.G. (1969a) Weight dynamics of Eucalyptus in the mallee vegetation of south-east Australia. Ecology 50: 212-219.

Holland, P.G. (1969b) The plant patterns of different seasons in two stands of mallee vegetation. J. Ecol. 57: 323-333.

Holland, P.G. (1969c) The maintenance of structure and shape in three mallee eucalypts. New Phytol. 68: 411-421.

Holling, C.S. (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91:293-320.

Hsiao, T.C. (1973) Plant responses to water stress. Ann. Rev. Plant Physiol. 24: 519-570.

Ioannou, N. (1968) A study of historical effects on the vegetation of the marginal lands. B.Sc. (hons.) Thesis, Univ. of Adelaide.

Jacobs, M.R. (1955) Growth Habits of the Eucalypts. Government Printer, Canberra.

Janzen, D.H. (1969) Seed eaters versus seed size, number, toxicity and dispersal. Evolution 23:1-27.

Janzen, D.H. (1971) Seed predation by animals. Ann. Rev. Ecol. Syst. 2:465-492.

Jessup, R.W. (1946) The ecology of the area adjacent to Lakes Alexandrina and Albert. Trans. Roy. Soc. S. Aust. 70: 3-34.

Kenyon, A.S. (1914) The "mallee" country of north-western Victoria. Brit. Assoc. Adv. Sci. Rep. 84th Meeting pp. 442-443.

Kerr, L.R. (1925) The lignotubers of eucalypt seedlings. Proc. Roy. Soc. Vict. 37: 79-97.

Ladiges, P.Y. (1974) Variation in drought tolerance in Eucalyptus viminalis Labill. Aust. J. Bot. 22: 489-500.

Land Conservation Council (1974) Report on the Mallee Study Area, Land Conservation Council, Victoria.

Lange, O.L. (1975) Plant water relations. Progress in Botany 37: 78-97.

Larsen, E. (1965) Germination of Eucalyptus seed. Comm. Aust. For. Timb. Bur. Leaflet No. 94.

Lawrence, C.R. (1966) Cainozoic stratigraphy and structure of the Mallee region, Victoria. Proc. Roy. Soc. Vict. 79:517-554.

Leeper, G.W. (1967) Introduction to Soil Science. Melb. Univ. Press, Melbourne.

Leeper, G.W. (1970) Climates. In: The Australian Environment (Ed. G.W. Leeper) 4th Ed. pp. 12-20. Melb. CSIRO.

Levitt, J. (1972) Responses of Plants to Environmental Stress. Academic Press, New York.

Majer, J.D. (1980) Report on a study of invertebrates in relation to the Kojonup Fire Management Plan. W.A.I.T. Dept. Biology, Bulletin No. 2.

McArthur, A.G. (1968) The fire resistance of eucalypts. Proc. Ecol. Soc. Aust. 3: 83-90.

McCracken, D.D. and Dorn, W.S. (1964). Numerical Methods and Fortran Programming. Wiley, New York.

Meinig, D.W. (1962) On the Margins of the Good Earth. John Murray, London.

Miller, H.P. and Perry, R.A. (1968) Preliminary studies on the establishment of Townsville lucerne (Stylosanthes humilis) in uncleared native pasture at Katherine, N.T. Aust. J. Exp. Agric. Anim. Husb. 8:26-32.

Mooney, H.A., Ferrar, P.J. and Slatyer, R.O. (1978) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of Eucalyptus. Oecol. 36:103-112.

Morrow, P.A. and LaMarche, V.C. (1978) Tree ring evidence for chronic insect suppression of productivity in subalpine Eucalyptus. Science 201:1244-1246.

Morton, S.R. (1980) Granivory in the Australian arid zone: diversity of harvester ants and structure of their communities. Unpublished manuscript.

Mott, J.J. (1974) Factors affecting seed germination in three annual species from an arid region of Western Australia. J. Ecol. 62: 699-709.

Mullette, K.J. (1978) Studies of the lignotubers of Eucalyptus gummifera (Gaertn. & Hochr.). I. The nature of the lignotuber. Aust. J. Bot. 26: 9-13.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. and Brent, D.H. (1975). Statistical Package for the Social Sciences. McGraw-Hill, Inc. U.S.A.

Noble, I.R. and Crisp, M.D. (1980) Germination and growth models of short-lived grass and forb populations based on long term photo-point data at Koonamore, South Australia. Israel. J. Bot. 28: 195-211.

Noble, I.R. and Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio, 43:5-21.

Noble, J.C., Smith, A.W. and Leslie, H.W. (1980) Fire in the mallee shrublands of western New South Wales. Aust. Rangel. J. 2: 104-114.

Noy-Meir, I. (1970) Component analysis of semi-arid vegetation in south-eastern Australia. Ph.D. Thesis, Aust. Nat. Univ.

Noy-Meir, I. (1971) Multivariate analysis of the semi-arid vegetation in south-eastern Australia: I Nodal ordination by component analysis. Proc. Ecol. Soc. Aust. 6: 159-193.

Noy-Meir, I. (1974) Multivariate analysis of the semi-arid vegetation in south-eastern Australia: II Vegetation catenae and environmental gradients. Aust. J. Bot. 22: 115-140.

O'Dowd, D.J. and Gill, A.M. (1980) Induction of massive, synchronized seedfall in Eucalyptus delegatensis by fire. Aust. Seed Sci. Newslett. 6: 21-22.

Ogden, J. (1978) On the dendrochronological potential of Australian trees. Aust. J. Ecol. 3: 339-356.

Parsons, R.F. (1966) The edaphic ecology of three mallee species of Eucalyptus. Ph.D. Thesis, Univ. of Melb.

Parsons, R.F. (1968a) An introduction to the regeneration of mallee eucalypts. Proc. Roy. Soc. Vict. 81: 59-68.

Parsons, R.F. (1968b) Distribution and paleogeography of two mallee species of Eucalyptus in southern Australia. Aust. J. Bot. 17 (2): 323-330.

Parsons, R.F. (1968c) Ecological aspects of the growth and mineral nutrition of three mallee species of Eucalyptus. Oecol. 3: 121-136.

Parsons, R.F. (1970) Mallee vegetation of the southern Nullabor and Roe plains, Australia. Trans. Roy. Soc. S. Aust. 94: 227-241.

Parsons, R.F. and Rowan, J.N. (1968). Edaphic range and cohabitation of some mallee eucalypts in south-eastern Australia. Aust. J. Bot. 16 (1): 109-116.

Pearl, R. and Miner, J.R. (1935) Experimental studies on the duration of life. XIV The comparative mortality of certain lower organisms. Quart. Rev. Biol. 10: 60-79.

Pescott, E.E. (1941) Germination of the seed of mallee eucalypts. Vict. Nat. 58: 8.

Peters, D.B. (1965) Water availabiliy. In: Methods of Soil Analysis. Part 1. Physical and Mineralogical Properties. (Editor in chief: C.A. Black) p281 Amer. Soc. Agron. Washington, U.S.A.

Polach, H.A. (1975) Radiocarbon dating as a research tool in archaeology - hopes and limitations, in Proceedings of the Symposium on Ancient Chinese Bronzes and other Archeological Artefacts, Ed. N. Barnard, National Gallery of Victoria, Melbourne, pp 225-298.

Porter, J.W. (1975) A relation between honey production and rainfall in Victoria, Australia. Vict. Nat. 92: 270-272.

Pryor, L.D. (1960) The 'ashbed' effect in eucalypt ecology. Inst. For. Aust. Newslett. 2: 23-26.

Pryor, L.D. and Johnson, L.A.S. (1971) A Classification of the Eucalypts. Aust. Nat. Univ., Canberra.

Purdie, R.W. (1976) Ecological succession after burning in dry sclerophyll vegetation. Ph.D. Thesis, Aust. Nat. Univ.

Purdie, R.W. (1977) Early stages of regeneration after burning in dry sclerophyll vegetation. II. Regeneration by seed germination. Aust. J. Bot. 25: 35-46.

Rabotnov, T.A. (1969) On coenopopulations of perennial herbaceous plants in natural coenoses. Vegetatio 19: 87-95.

Rayson, P. (1957) Dark Island heath (Ninety-Mile Plain, South Australia). II. The effects of microtopography on climate, soils and vegetation. Aust. J. Bot. 5: 86-102.

Renbuss, M.A., Chilvers, G.A. and Pryor, L.D. (1972) Microbiology of an ashbed. Proc. Linn. Soc. N.S.W. 97: 302-310.

Ritchie, G.A. and Hinckley, T.M. (1975) The pressure chamber as an instrument for ecological research. Adv. Ecol. Res. 9: 165-256.

Rowan, J.N. and Downes, R.G. (1963) A study of the land in north-western Victoria. Soil Conserv. Auth. Vict. Tech. Comm. No. 2.

Scholander, P.F., Hammel, H.T., Bradstreet, E.D. and Hemmingsen, E.A. (1965). Sap pressure in vascular plants. Science, N.Y. 148: 339-346.

Scott, L. (1972) Viability testing of eucalypt seeds. Comm. Aust. For. Timb. Bur. Leaflet No. 116.

Sims, H.J. (1951) The natural regeneration of some trees and shrubs at Walpeup, Victorian mallee. Vict. Nat. 68: 27-30.

Smith, G.G., Williams, K.M. and Wonnacott, D.M. (1978) Factors affecting the rate of racemization of amino acids and their significance to geochronology. J. Org. Chem. 43: 1-5.

Sokal, R.R. and Rohlf, F.J. (1969) Biometry. W.H. Freeman and Co., San Francisco.

Specht, R.L. (1957a) Dark Island heath (Ninety-Mile Plain, South Australia) IV. Soil moisture patterns produced by rainfall interception and stem flow. Aust.J.Bot. 5: 137-150.

Specht, R.L. (1957b) Dark Island heath (Ninety-Mile Plain, South Australia) V. The water relationships in heath vegetation and pastures on the Makin sand. Aust. J. Bot. 5: 151-172.

Specht, R.L. (1972) The Vegetation of South Australia. 2nd Ed., Govt. Printer, Adelaide.

Specht, R.L. and Rayson, P. (1957a) Dark Island heath (Ninety-Mile Plain, South Australia) I. Definition of the ecosystem. Aust. J. Bot. 5: 52-85.

Specht, R.L. and Rayson, P. (1957b) Dark Island heath (Ninety-Mile Plain, South Australia) III. The root systems. Aust. J. Bot. 5: 103-114.

Stace, H.C.T., Hubble, G.D., Brewer, R., Northcote, K.H., Sleeman, J.R., Mulcahy, M.J. and Hallsworth, E.G. (1968) A Handbook of Australian Soils. Rellim Technical Publications, Glenside, S.A.

Stannard, M.E. (1958) Erosion survey of the south-west Cobar peneplain. II Soils and vegetation. J. Soil Cons. Serv. N.S.W. 14: 30-45.

Stiles, W. Monteith, J.L. and Bull, T.A. (1970). A diffusive resistance porometer for field use. J. Appl. Ecol. 7: 617-638.

Suiter, W. and Lisbao, L. (1973) Influence of relative humidity on the characteristics of the seeds of Eucalyptus saligna Sm. Proc. Internat. Symp. Seed Processing, Bergen, Norway, Vol. II, paper No. 10.

Turner, N.C., Pederson, F.C.C. and Wright, W.H. (1969) An aspirated diffusion porometer for field use. Special Soils Bull. Conn. Agric. Exp. Stn. No. XXIX.

Warcup, J.H. (1980) Effect of heat treatment of forest soil on germination of buried seed. Aust. J. Bot. 28: 567-571.

Watt, A.S. (1923) On the ecology of British beechwoods, with special reference to their regeneration. I. The causes of failure of natural regeneration of the beech (Fagus silvatica L.) J. Ecol. 11: 1-48.

Wellington, A.B., Polach, H.A. and Noble, I.R. (1979) Radiocarbon dating of lignotubers from mallee forms of Eucalyptus. Search 10: 282-283.

Willis, J.H. (1972) A Handbook to Plants in Victoria. Vol. 2: Dicotyledons. Melb. Univ. Press, Melbourne.

Wong, S.C. (1979) Stomatal behaviour in relation to photosynthesis. Ph.D. Thesis, Aust. Nat. Univ.

Wong, S.C., Cowan, I.R. and Farquhar, G.D. (1979). Stomatal conductance correlates with photosynthetic capacity. Nature 282: 424-426.

Wood, J.G. (1929) Floristics and ecology of the mallee. Trans. Roy. Soc. S. Aust. 53: 359-378.

Yoda, K., Hira., T., Ogawa, H. and Hozumi, K. (1963) Self thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka Cy. Univ. 14: 107-129.

Zimmer, W.J. (1940a) Plant invasions in the mallee. Vict. Nat. 56: 143-147.

Zimmer, W.J. (1940b) Can mutilated forest types in the far north-west of Victoria be rehabilitated? Vic. For. 2: 35-37.

Zimmer, W.J. (1941) Some notes on the germination of mallee eucalypts. Vict. Nat. 58: 61-62.

Zimmer, W.J. (1946) The flora of the far north-west of Victoria. For. Comm. of Vict. Bull. No. 2.

Zimmer, W.J. and Grose, R.J. (1958) Root systems and root/shoot ratios of seedlings of some Victorian eucalypts. Aust. For. 22: 13-18.

APPENDIX 1 : Published report of radiocarbon dating of mallee lignotuber wood (Chapter 2)

Radiocarbon Dating of Lignotubers from Mallee Forms of *Eucalyptus*

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The multi-stemmed form of *Eucalyptus* known as mallee, found in several different habitats throughout Australia, is particularly common over large areas of the drier southern regions of the continent (Wood, 1929). Mallees possess a well-developed, semi-subterranean, woody mass of stem tissue called a lignotuber (Kerr, 1925), which is able to survive severe environmental stresses, including recurrent fire (Zimmer, 1940; Jacobs, 1955; Chattaway, 1958; McArthur, 1968). The lignotuber has a large number of cortical buds from which new stems develop (Chattaway, 1958).

The large size attained by some lignotubers (> 2 metres diameter), their ability to survive severe environmental stresses, and the rarity of natural seedling regeneration (Holland, 1968; Parsons, 1968), led to speculation that lignotubers may attain ages of 500 years or more (Holland, 1968; Gill 1971; Ogden, 1978). However, their lack of any regular structural or growth features (Kerr, 1925; Chattaway, 1958; Carrodus and Blake, 1970) limits the use of methods other than ^{14}C dating for determining their age. The only published radiocarbon age determination of a lignotuber sample (NZ-32) was made using wood from the centre of a large (~ 1.2 m diameter) lignotuber of the mallee *Eucalyptus oleosa*, and yielded a 'modern' (< 200 years) age (Grant Taylor and Rafter, 1963).

Radiocarbon age estimates of further samples are necessary to verify this result. Four lignotubers, thought to be amongst the oldest in their respective populations, were collected from two sites near Balranald in south-western New South Wales (site A: 34°27′ S, 142°51′ E; site B: 34°38′S, 143°15′ E). Eight samples were analyzed for ^{14}C content: a single sample was taken from each of three lignotubers (ANU-1991 to 1993) and the remaining samples from the fourth (Table 1, Figure 1).

Six samples (ANU 1991 to 1996) were treated prior to ^{14}C analysis using a technique designed to remove all substances except the cellulose and hemi-cellulose components of the cell walls (Olson and Broecker, 1958). Two samples (ANU-2011 and 2033) were not pre-treated, so that carbon from other cell wall materials and from any substances stored in the wood was included in the ^{14}C determinations.

The results obtained for ANU-1992 to 1996 and ANU-2011, agree with the earlier age estimate (Grant Taylor and Rafter, 1963). The radiocarbon age of ANU-1991 was 330 ± 70 years BP. However, ANU-1991 was taken from wood remnants buried below a fragmented lignotuber of *E. oleosa*. The remnants were not attached to any living lignotuber segments and the possibility that they originated from another long-dead lignotuber cannot be excluded. Sample ANU-2033, taken from the sapwood interior to the cambium and not pretreated, showed a greater than 100% 'modern' radiocarbon age and therefore contained carbon assimilated since 1950 (see Polach, 1975).

Radiocarbon concentration determinations of treated (ANU-1996) and untreated (ANU-2011) heartwood from comparable locations in a lignotuber (Figure 1) gave 'indicated ages' of 70 ± 60 years BP and 10 ± 60 years

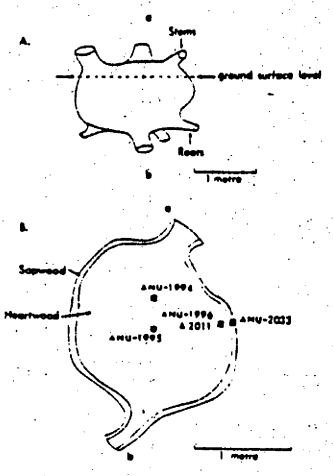

FIGURE 1

Lignotuber used for radiocarbon analysis (samples ANU-1994 to 6, ANU-2011, ANU-2033). (A) Overall sketch of lignotuber showing plane of section (a-b). (B) Sketch of longitudinal section showing location of samples.

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TABLE 1
Results of ^{14}C determinations

Sample No.	Site	Nature of sample	^{14}C age*
ANU-1991	A	Decayed wood remnants buried below a fragmented lignotuber of *E. oleosa*. Wood remnants buried in soil; not attached to living segments. Age determination on 'cellulose'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = −40.4 ± 7.5‰ Age = 330 ± 70 BP
ANU-1992	A	Decaying wood attached to a large (125 cm. diam.) separate, living lignotuber of *E. oleosa*. Age determination on 'cellulose'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = −19.4 ± 7.2‰ Age = 'modern' 'Ind. age' = 160 ± 60 BP
ANU-1993	B	Heartwood from central regions of large (150 cm. diam.) separate, living lignotuber of *E. oleosa*. (Aerial parts destroyed during agricultural clearing; identified from heartwood characteristics.) Age determination on 'cellulose'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = −12.8 ± 7.3‰ Age = 'modern' 'Ind. age' = 105 ± 60 BP
ANU-1994	B	Heartwood from upper-central regions of major root-shoot axis (see Fig. 1) in centre of large (180 cm. diam.) separate, living lignotuber of *E. oleosa* (Aerial parts destroyed during agricultural clearing; identified from heartwood characteristics.) Age determination on 'cellulose'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = −23.1 ± 7.2‰ Age = 'modern' 'Ind. age' = 190 ± 60 BP
ANU-1995	B	Sample taken from same lignotuber as ANU-1994 but located in lower central regions nearer root (see Fig. 1). Age determination on 'cellulose'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = −22.3 ± 7.3‰ Age = 'modern' 'Ind. age' = 185 ± 60 BP
ANU-1996	B	Sample taken from same lignotuber as ANU-1994 but located in heartwood ~ 8 cm from periphery (see Fig. 1). Age determination on 'cellulose'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = − 8.5 ± 7.3‰ Age = 'modern' 'Ind. age' = 70 ± 60 BP
ANU-2011	B	Comparable to ANU-1996. Age determination on sample 'as is'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = − 1.2 ± 7.9‰ Age = 'modern' 'Ind. age' = 10 ± 60 BP
ANU-2033	B	Sample taken from same lignotuber as ANU-1994 but located in the sapwood, interior to the cambium. Age determination on sample 'as is'.	Est. $\delta^{13}C$ = −24.0 ± 2.0‰ $D^{14}C$ = +363.9 ± 8.8‰ Age = '> modern'

*Ages BP are expressed as *conventional radiocarbon ages* — i.e., based on Libby ^{14}C half-life of 5570 years, and corrected for isotopic fractionation ($\delta^{13}C$). $D^{14}C‰$ = millesimal difference in ^{14}C count-rate of standard (.95 NBSOx) and sample.
'Indicated ages' are based on $D^{14}C‰$ depletion (Stuiver and Polach, 1977).

BP respectively. These results demonstrate that there is no age difference between the structural cellulose of the outer heartwood and the substances stored in the cellulose structure, and therefore support the hypothesis that contamination by younger carbon from substances stored in the wood is unlikely to have significantly altered the ^{14}C estimates obtained.

A comparison of the results for samples ANU-2011 and ANU-2033 indicates a significant age difference between wood taken from regions of the lignotuber 5 cm apart, but separated by the sapwood-heartwood boundary. However, samples taken from the heartwood (ANU-1994 to 1996, and ANU-2011) and separated by 80 cm along a radius yielded no significant difference in radiocarbon age, although the 'indicated ages', based on ^{14}C concentration as expressed by the $D^{14}C$ values, do show that the centrally-located heartwood replicates (ANU-1994: 190 ± 60 BP, ANU-1995: 185 ± 60 BP) are slightly older than the peripheral heartwood samples (ANU-1996 and 2011). Observations made on stem tissues indicate that there is no significant movement of substances across the sapwood-heartwood boundary (Stewart, 1966). The results obtained for ANU-1994 to 1996, ANU-2011 and ANU-2033 support these observations for lignotuber tissues and further support the hypothesis that the ^{14}C estimates are not biased by the presence of younger carbon.

Other sources of contamination (see Polach, 1975) are considered unlikely to have influenced the results and the radiocarbon age estimates obtained appear to be reliable for lignotuber wood. We therefore confirm the radiocarbon estimate of Grant Taylor and Rafter (1963) and conclude that the lignotuber wood of large, living specimens of the mallee *Eucalyptus oleosa* is younger than 200 years BP.

References

CARRODUS, B.B. and BLAKE, T.J. (1970) Studies on the lignotuber of *Eucalyptus oblique* l'Herit. I. The nature of the lignotuber. *New Phytol.*, 19, 1069-72.

CHATTAWAY, M.M. (1958) Bud development and lignotuber formation in eucalypts. *Aust. J. Bot.*, 6, 103-15.

GILL, E.D. (1971) Applications of radiocarbon dating. *Proc. R. Soc. Vict.*, 84, 71-86.

GRANT TAYLOR, T.L. and RAFTER, T.A. (1963) N.Z. natural radiocarbon measurements I-V. *Radiocarbon*, 5, 118-161.

HOLLAND, P.G. (1968) Seasonal growth of field layer plants in two stands of mallee vegetation. *Aust. J. Bot.*, 16(3), 615-622.

JACOBS, M.R. (1955) *Growth Habits of the Eucalypts*, Govt. Printer, Canberra.

KERR, L.R. (1925) The lignotubers of eucalypt seedlings. *Proc. R. Soc. Vict.*, 16, 79-97.

McARTHUR, A.G. (1968) Fire resistance of eucalypts. *Proc. Ecol. Soc. Aust.*, 3, 83-90.

OGDEN, J. (1978) On the dendrochronological potential of Australian trees. *Aust. J. Ecol.*, 3, 339-356.

OLSON, E.A. and BROECKER, W.S. (1958) Sample contamination and reliability of ^{14}C dates. *Trans. N.Y. Acd. Sci.* (Series 2), 20(7), 593-604.

PARSONS, R.F. (1968) An introduction to the regeneration of mallee eucalypts. *Proc. Roy. Soc. Vict.*, 81, 59-68.

POLACH, H.A. (1975) Radiocarbon dating as a research tool in archaeology — hopes and limitations, in *Proceedings of the Symposium on Ancient Chinese Bronzes and other Archeological Artefacts*, Ed. N. Barnard, National Gallery of Victoria, Melbourne, 225-298.

STEWART, C.M. (1966) Excretion and heartwood formation in living trees. *Science*, 153, 1068-74.

STUIVER, M. and POLACH, H.A. (1977) Discussion: reporting of ^{14}C data. *Radiocarbon*, 19, 355-363.

WOOD, J.G. (1929) Floristics and ecology of the mallee. *Trans. & Proc. R. Soc. S.A.*, 53, 359-368.

ZIMMER, W.J. (1940) Plant invasions in the mallee. *Vict. Nat.*, 56, 143-147.

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